
POLLINATION BIOLOGY IN A TROPICAL HIGH-ALTITUDE GRASSLAND IN BRAZIL: INTERACTIONS AT THE COMMUNITY LEVEL^{1,2}

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ABSTRACT

Surveys of local assemblages of plants and their pollinators are among the most useful ways to evaluate specialization in pollination and to discuss the patterns of plant-pollinator interactions among ecosystems. The high-altitude grasslands from southeastern Brazil constitute diminutive island-like formations surrounded by montane rainforests. We registered the floral traits of 124 species from the Serra da Bocaina grasslands (about 60% of the animal-pollinated species of this flora), and determined the pollinators of 106 of them. Asteraceae (10 species) and Melastomataceae (10 species) were prominent, while most families were represented by few species. The predominant floral traits were: dish or short-tubular shape; nectar as a reward; and greenish or violaceous colors. Pollinators were divided into eight functional groups (small bees, syrphids, other dipterans, etc.) and small bees, wasps, and large bees were the most important pollinators. Butterflies, beetles, and hummingbirds were poorly represented, and no bats, hawkmoths, or odor-collecting bees were detected. Plants were grouped in nine pollination systems, among which nectar-flowers pollinated by bees (28%), by wasps or wasps and flies (21%), or by several insect groups (19%) were the most representative. With regard to the degree of specialization, plant species were classified according to their number of pollinator groups. About 33% of the species were monophilous and 30% were oligophilous (i.e., pollinated by one or two functional groups, respectively). The remaining species were either polyphilous (17%) or holophilous (19%), a highly generalist system in which at least three groups act as indistinct pollinators. The general trends of the floral traits and plant-pollinator interactions at the Bocaina grasslands resemble those of biogeographic-connected ecosystems, such as the Venezuelan *arbustal*, and the Brazilian *campo rupestre* and *cerrado*. However, in the Bocaina grasslands, the mean number of pollinator types per plant was 2.09, one of the highest values obtained for worldwide floras. The origin of the high-altitude grasslands is linked to episodes of expansion and retraction due to glacial events. Such a situation may have favored species able to quickly occupy new habitats, including those that do not depend on a few highly specialized pollinators. The prevalence of Asteraceae may also be linked to more generalized pollination systems. Alternatively, some floral traits, such as spontaneous self-pollination and long-lived flowers, may be advantageous for species with more specialized systems in these grasslands with harsh climatic conditions and low rates of pollinator visitation.

Key words: Asteraceae, bees, biogeography, floral biology, generalization, pollination ecology, specialization, syndrome, wasps.

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Plant reproductive processes are believed to help determine the composition and structure of communities (Heithaus, 1974, 1979; Bawa, 1990; Oliveira & Gibbs, 2000). Among such processes, the plant-pollinator interactions form a dynamic, yet somewhat cohesive, ecological subunit of a community, which can be studied in terms of species diversity and distribution, resource utilization, and niche packing, for instance (Moldenke & Lincoln, 1979). In the Neotropics, pollination biology at the community level has been studied in forest areas (Bawa et al., 1985; Kress & Beach, 1994), savanna-like vegetation (Silberbauer-Gottsberger & Gottsberger, 1988; Ramírez, 1989, 2004; Barbosa, 1997; Oliveira & Gibbs, 2000; see also Ramírez & Brito, 1992) and sub-Andean vegetation (Arroyo et al., 1982). In the Brazilian Atlantic Forest Domain, there are several studies on pollination biology in forest areas on both individual species and flower assemblages (Sazima et al., 1995, 1996, 1999; Buzato et al., 2000 and references therein). However, for the high-altitude grasslands or *campos de altitude*—a subtype of the Atlantic Forest Domain—information on plant-pollinator interactions is limited to a few case studies (Martinelli, 1997; Freitas & Sazima, 2001, 2003a, b; Freitas et al., 2006).

The high-altitude grasslands in southeastern Brazil comprise an archipelago of mountaintop formations (ca. 1500 m elevation or higher) along the main mountain ranges, with a North/South orientation. Their origin is connected to glaciation episodes since at least the Late Pleistocene, when these grassland areas are supposed to have experienced periods of expansion and retraction (Ledru et al., 1998). The present high-altitude grasslands have strong biogeographic connections with other high-altitude ecosystems in South America, such as the Andean and Central-American (sub-) alpine habitats, as well as with the Central–Eastern Brazilian rocky and grassy habitats (*campo rupestre*) (Giulietti & Pirani, 1988; Safford, 1999a and references therein). They are also connected to the central Brazilian savannas (*cerrado*) (Silveira & Cure, 1993; see also Modenesi, 1988 for *cerrado* components in palinofloras from the grasslands). These grasslands present—for such restricted areas of habitat—extraordinarily rich floras with many endemics. About one third of the ca. 400 species of the Itatiaia plateau (< 50 km²), for instance, appear to be endemic to the high-altitude grasslands (Martinelli, 1989). However, many species on the high-altitude grasslands have small populations with few individuals. Owing to such features as high species richness, high endemism, small populations, “island-like” occurrence, biogeographic connections, and harsh climatic conditions for a tropical place, the

Brazilian high-altitude grasslands are interesting communities in which to study plant-pollinator interactions.

In pollination biology, the degree of specialization in plant-pollinator relationships has generated a debate in which the traditional view based on the syndrome concept (see Faegri & van der Pijl, 1979) has been counterbalanced by skepticism about the specialized nature of pollination systems (Waser et al., 1996; Herrera, 1996; see also Johnson & Steiner, 2000 and Fenster et al., 2004 for reviews of both views). Surveys of entire local assemblages of plants and their pollinators provide the best evidence to assess the degree of specialization in pollination (Waser et al., 1996), because particular plant-pollinator interactions may be examined on a broad ecological scale, reducing the sampling bias inherent to the comparison of data originating from small scale studies, such as those concerning particular plant taxonomic groups. This paper describes the community-level interactions between plants and pollinators of high-altitude grasslands at the Serra da Bocaina, southeastern Brazil. We studied the floral biology of plant species, recording their sexual systems, flower shapes, dimensions, resources, colors, and pollinators. Combining the data on floral features and functional groups of pollinators allowed us to characterize nine pollination systems in these grasslands and to group plant species in four categories that express the degree of specialization/generalization of plant-pollinator interactions in this community. In addition, we monitored the flowering phenology so as to assess flower resource availability, throughout the year, for the main pollinator groups. We provide a discussion about general patterns of plant-pollinator interactions at the Serra da Bocaina grasslands in relation to other ecosystems with strong biogeographic connections, as well as in relation to the current debate about the prevalence of generalization versus specialization in the plant-pollinator interactions.

AREA AND VEGETATION STUDIED

The Parque Nacional da Serra da Bocaina (PNSB)—ca. 100,000 hectares—is located between the States of Rio de Janeiro and São Paulo, in southeastern Brazil. Since it extends from sea level to the highest peaks in the Serra da Bocaina (ca. 2100 m), the PNSB shelters many vegetation types of the Brazilian Atlantic Forest Domain. The lower areas are covered mainly by lowland and submontane rainforest, followed by montane and high-altitude forest. Originally, these high-altitude grasslands probably occurred only above 1700–1800 m, but nowadays, due to human disturbance of the forested

areas, they can be found from as low as ca. 1450 m. These grasslands are composed of a matrix of Poaceae and Cyperaceae species mixed with shrubs and herbs from many families, mainly Asteraceae and Melastomataceae. Scattered small trees, mainly species belonging to the genus *Eremanthus* Less. (Asteraceae), can also be found in more protected fields.

In southeastern Brazil, the montane areas encompass two climate regions (Köppen, 1948). Grasslands from the highest summits (above ca. 2000 m) are Cwb, with $\leq 12^{\circ}\text{C}$ mean annual temperature, cool summers, moderately cold winters with frequent frost, and rare snow. Montane areas at lower elevations can be classified as Cfb (Cwb and Cfb as in Köppen, 1948), i.e., mesothermic, with 12°C – 20°C average annual temperature, moderate winters, and mild, wet summers (Segadas-Vianna & Dau, 1965; Nimer, 1977; Safford, 1999a, b). Most grassland areas at Serra da Bocaina are Cfb. Annual precipitation is up to 2100 mm. Rains are concentrated in summer, mainly from December to March. The dry season (Apr. to Sept.) is driest from June to August, with precipitation < 50 mm per month. The effects of seasonal drought on the vegetation are partially offset by thick banks of orographic fog that shroud most Bocaina grasslands, mainly in the early morning, for much of the year. Annual mean temperature is ca. 15°C at 1500–1600 m, and minimum temperatures around 0°C are common during winter (L. Freitas, pers. obs.). During the study period (1998–1999), frosts occurred on more than 30 days per year (L. Freitas, pers. obs.). General information about the vegetation, climate, and topography of southeastern Brazil is available in Segadas-Vianna & Dau (1965), Eiten (1970, 1992), Alonso (1977), Nimer (1977), Moreira & Camelier (1977), and Safford (1999a, b).

Despite its long history in Bocaina highlands, human disturbance was low until the beginning of the 20th century. The primary source of revenue of the inhabitants of this region comes from livestock. Regular fires and grazing are supposed to have negative impacts on the physical environment, the vegetation structure and dynamics, and the welfare of some of the small and endemic plant populations of these grasslands (Safford, 1999a, but see Safford, 2001). Natural fires are apparently rare on these grasslands and are restricted to the wet season, when lightning occurrence is frequent. Anthropogenic fires, however, are frequently set during the dry season, because such an action favors the sprouting of grasses after the rains begin. Some plants may have been eliminated by these regular fires, in particular, species restricted to mesic habitats. However, many of the typical high-altitude taxa, such as the geophytes, have a strong capacity to sprout, appar-

ently as a pre-adaptation against frost, that also seems to be efficient against fires.

This study was carried out in three grassland sites that experienced different fire regimes over the years. Since there is no official register of fire occurrences, information for the last 45–50 years was obtained from both the PNSB staff and the inhabitants of the region. The first area ($22^{\circ}43'57''\text{S}$, $44^{\circ}37'06''\text{W}$) is adjacent to a private farm (Fazenda Mariana) and used to burn every two to three years. The last fire in that area had occurred ca. five months before the beginning of this study (Dec. 1997). The second area ($22^{\circ}44'50''\text{S}$, $44^{\circ}36'57''\text{W}$) is close to Santo Izidro waterfall and used to burn at intervals of five to 10 years. The last fire in this area had occurred five years before the first year of this study, and the area burned again in 1998. Since it presented many treelets and large shrubs, the third area ($22^{\circ}44'12''\text{S}$, $44^{\circ}36'55''\text{W}$) showed marked structural differences. There was no record of fire here when the project started, but the area burned in September 1999.

About 260 plant species belonging to 46 families were recorded during monthly collections in the three study areas and through non-systematic collections in other grassland areas located between 1450 m and 2100 m. Although most families were only represented by a few species, some families, such as Asteraceae (ca. 70 spp.), Poaceae (ca. 35 spp.), Cyperaceae (ca. 15 spp.), Melastomataceae (18 spp.), Orchidaceae, Iridaceae, Rubiaceae, and Solanaceae, were common. Most species were herbs or (sub)shrubs, with small, often lignified and hairy leaves. Many species had leaves with a cupressoid or rosette arrangement, and several perennial plants showed well-developed underground organs (e.g., *Tibouchina minor*, *Microlicia isophylla*, *Esterhazyia macrodonta*, *Escallonia farinacea*). Such vegetative features are typical of plants living in high-altitude tropics (Camerik & Werger, 1981; Smith & Young, 1987; Safford, 1999a).

MATERIAL AND METHODS

Between December 1997 and February 2000, we made 25 field trips to Serra da Bocaina, for a total of 211 days of fieldwork. Pollination biology at the community level was studied along a transect ca. 1 km long in each of the three study sites. We studied all plant species located within 5 m of the transects, except Cyperaceae and Poaceae (Table 1). The following floral attributes were noted in the field: shape, symmetry, size, color, and rewards (Table 2). Following Faegri and van der Pijl (1979) and Endress (1994), the flowers were classified into eight different types: inconspicuous, dish (bowl), brush, bell (funnel), flag, gullet, tube, and revolver. Tube types include

Table 1. Plant species, their habit, flowering time, and flowering peak at the Serra da Bocaina grasslands. All collections by the authors are deposited at the UEC, and the collection number (L. Freitas) follows the taxon name in parentheses. Phenological observations occurred from January to December 1999. Species that were found only in the area that burnt in September 1999 are indicated by the symbol (f).

Family/Species	Habit	Flowering time	Flowering peak
Amaryllidaceae			
<i>Hippeastrum glaucescens</i> Mart. (773)	herb	Oct.–Nov.	Nov.
Apiaceae			
<i>Eryngium canaliculatum</i> Cham. & Schltdl. (792)	herb	Nov.–Dec.	Dec.
<i>Eryngium horridum</i> Malme (140)	herb	Jan.–Mar.	Jan.
Apocynaceae			
<i>Gonioanthela hilariana</i> (E. Fourn.) Malme (329)	vine	Mar.–July (f)	Mar.–May
<i>Mandevilla erecta</i> (Vell.) Woodson (86, 509)	sub-shrub	Jan.–Feb.	Jan.
<i>Oxypetalum appendiculatum</i> Mart. (123)	vine	Jan.–Aug. (f)	Apr.–June
<i>Oxypetalum sublanatum</i> Malme (13, 491)	vine	Jan., Mar.–May, Oct.–Dec.	Jan., Apr., Nov.–Dec.
<i>Tassadia subulata</i> (Vell.) Fontella & E. A. Schwarz (686)	vine	May–Aug.	June
Aquifoliaceae			
<i>Ilex amara</i> (Vell.) Loes. (656, 797)	sub-shrub	Nov.–Dec.	Nov.–Dec.
Asteraceae			
<i>Achyrocline satureioides</i> (Lam.) DC. (276, 330)	shrub	Jan.–Aug., Dec.	Mar.–June
<i>Baccharis aphylla</i> (Vell.) DC. (707)	sub-shrub	Sep.–Nov.	Sep.–Oct.
<i>Baccharis curitybensis</i> Heering & Dusen (498)	sub-shrub	Jan.–Mar., Dec.	Jan.
<i>Baccharis dracunculifolia</i> DC. (372)	shrub	Mar.–Oct.	Apr.–May, Aug.
<i>Baccharis intermixta</i> Gardner (418)	shrub	May–Aug.	July
<i>Baccharis leptcephala</i> DC. (392, 443, 688)	herb	Apr.–Sep.	May–Aug.
<i>Baccharis pentziifolia</i> Sch. Bip. ex Baker (589, 691, 728)	shrub	Jan.–Dec.	Feb., May–Aug., Oct.–Nov.
<i>Baccharis platypoda</i> DC. (334, 863)	shrub	Mar.–June	May
<i>Baccharis tarchonanthoides</i> Baker (733)	sub-shrub	Oct.–Nov.	Oct.–Nov.
<i>Baccharis</i> L. sp. indet. 1 (407)	shrub	July–Aug.	July
<i>Baccharis</i> sp. indet. 2 (441, 689)	shrub	May–July	June–July
<i>Baccharis</i> sp. indet. 3 (108)	shrub	Jan.–Mar.	Jan.
<i>Barrosoa betoniciiiformis</i> (DC.) R. M. King & H. Rob. (512, 591)	herb	Jan.–May	Feb.–Mar., May
<i>Campuloclinium megacephalum</i> (Mart. ex Baker) R. M. King & H. Rob. (101, 596)	herb	Jan.–May	Feb.–Apr.
<i>Chaptalia integerrima</i> (Vell.) Burkart (744)	herb	Jan.–Feb., Oct.–Dec.	Oct.–Nov.
<i>Chaptalia runcinata</i> var. <i>graminifolia</i> (Dusen) Burkart (406, 697)	herb	May–Nov.	July–Aug.
<i>Chromolaena</i> cf. <i>decumbens</i> Gardner (100)	herb	Jan.–July	Jan.–Mar.
<i>Chromolaena xylorrhiza</i> (Sch. Bip. ex Baker) R. M. King & H. Rob. (835)	herb	Jan.–Feb.	Jan.
<i>Eremanthus erythropappus</i> (DC.) MacLeish (403)	treelet	Jul.–Aug. (f)	Aug.
<i>Erigeron maximus</i> (L. Don) Otto ex DC. (64)	shrub	Jan.–Mar., Oct.–Dec.	Jan.–Feb., Dec.
<i>Eupatorium</i> L. sp. indet. 1 (60, 61)	shrub	Jan., Nov.–Dec.	Nov.
<i>Eupatorium</i> sp. indet. 2 (99)	herb	Jan.–July, Dec.	Jan.–Feb.
<i>Eupatorium</i> sp. indet. 3 (326)	herb	Mar.–June	Apr.–May
<i>Eupatorium</i> sp. indet. 4 (374)	herb	Apr.	Apr.
<i>Gochnatia paniculata</i> (Less.) Cabrera (438, 705)	sub-shrub	Aug.–Nov.	Sep.–Oct.
<i>Grazielia gaudichaudeana</i> (DC.) R. M. King & H. Rob. (226, 590)	shrub	Jan.–June	Jan.–Feb.
<i>Hypochaeris gardneri</i> Baker (481)	herb	Jan.–Feb., Oct.–Dec.	Jan.–Feb., Nov.–Dec.
<i>Lucilia lycopodioides</i> (Less.) S. E. Freire (398, 838)	herb	June–Sep.	July–Aug.
<i>Mikania lundiana</i> DC. (393)	vine	May–Jul.	May

Table 1. Continued.

Family/Species	Habit	Flowering time	Flowering peak
<i>Mikania nummularia</i> DC. (440, 690)	shrub	May–Aug.	June–Aug.
<i>Mikania sessilifolia</i> DC. (318, 417, 871)	shrub	Mar.–May	Apr.
<i>Senecio oleosus</i> Vell. (391, 409)	shrub	Jan., Mar.–Sep., Nov.	Mar., July–Aug.
<i>Stevia myriadenia</i> Sch. Bip. ex Baker (88, 291)	shrub	Jan.–May	Feb.–Mar.
<i>Symphyopappus compressus</i> (Gardner) B. L. Rob. (57)	shrub	Jan.–Feb. (f)	Jan.
<i>Vernonia herbacea</i> (Vell.) Rusby (741)	herb	Oct.–Dec.	Nov.–Dec.
<i>Vernonia megapotamica</i> Spreng. (36, 536)	herb	Jan.–Apr.	Jan.–Feb.
<i>Vernonia</i> cf. <i>rosea</i> Mart. ex DC. (275, 592, 844)	sub-shrub	Jan.–Feb.	Feb.
<i>Vernonia tomentella</i> Mart. ex DC. (67, 588)	sub-shrub	Jan.–May, Oct.– Dec.	Jan.–Feb., Nov.–Dec.
<i>Vernonia tragiaefolia</i> DC. (626)	sub-shrub	Jan.–Feb., Apr.	Feb.
<i>Vernonia westiniana</i> Less. (92)	shrub	Jan.–June	Feb.
Bromeliaceae			
<i>Dyckia tuberosa</i> (Vell.) Beer (495)	herb	Sep.–Nov.	Oct.–Nov.
Campanulaceae			
<i>Lobelia camporum</i> Pohl (41)	herb	Jan.–June, Nov.– Dec.	Jan.–Feb., June, Dec.
<i>Wahlenbergia brasiliensis</i> Cham. (232, 280)	herb	Jan.–Dec.	Feb., June–Sep.
Clethraceae			
<i>Clethra scabra</i> Pers. var. <i>scabra</i> (332)	treelet	Feb.–Aug. (f)	Mar.–May
Convolvulaceae			
<i>Convolvulus crenatifolius</i> Ruiz & Pav. (37, 89)	vine	Jan.–Feb., Dec.	Jan., Dec.
<i>Ipomoea procumbens</i> Mart. (76)	vine	Jan.–Mar.	Feb.
<i>Jacquemontia grandiflora</i> Meisn. (118)	vine	Jan.–Aug., Nov.– Dec.	Jan.–Feb., May–July, Dec.
Cunoniaceae			
<i>Weinmannia organensis</i> Gardner (54, 125)	treelet	Jan.–Aug. (f)	Feb.–Mar., May
Droseraceae			
<i>Drosera montana</i> A. St.-Hil. (127)	herb	Jan.–Feb., Nov.– Dec.	Jan., Dec.
Ericaceae			
<i>Agarista hispidula</i> (DC.) Hook. f. ex Nied. (23, 431)	shrub	June–Nov.	Aug.–Sep.
<i>Gaylussacia chamissonis</i> Meisn. (469)	sub-shrub	Apr.–Dec.	Oct.–Dec.
<i>Gaylussacia jordanensis</i> Sleumer (370, 432)	sub-shrub	Jan.–May, Aug.– Dec.	Sep.–Oct.
Eriocaulaceae			
<i>Paepalanthus paulensis</i> Ruhland (706)	herb	Sep.–Dec.	Sep.–Nov.
<i>Paepalanthus polyanthus</i> (Bong.) Kunth (18)	herb	Jan.–June, Nov.– Dec.	Jan.–Apr., Dec.
Erythroxylaceae			
<i>Erythroxylum microphyllum</i> A. St.-Hil. (373, 496)	shrub	Jan.–May, Nov.– Dec.	Jan.–Feb., Dec.
Escalloniaceae			
<i>Escallonia farinacea</i> A. St.-Hil. (507)	shrub	Nov.–Dec.	Nov.
Euphorbiaceae			
<i>Croton dichrous</i> Müll. Arg. (17, 619)	shrub	Jan.–Dec.	Mar.–Jul., Nov.–Dec.
Gentianaceae			
<i>Calolisianthus pedunculatus</i> (Cham. & Schltdl.) Gilg (430, 520)	herb	Jan.–Apr., Dec.	Jan.–Feb.
<i>Calolisianthus pendulus</i> (Mart.) Gilg (80, 264)	herb	Jan.–May, July	Feb.
<i>Deianira nervosa</i> Cham. & Schltdl. (348)	herb	Feb.–Apr., June	Feb.–Mar.
<i>Helia oblongifolia</i> Mart. (1, 95)	herb	Jan.–Mar.	Jan.–Feb.
<i>Zygostigma australe</i> (Cham. & Schltdl.) Griseb. (622)	herb	Feb.–Apr.	Feb.–Mar.
Gesneriaceae			
<i>Sinningia allagophylla</i> (Mart.) Wiehler (9)	herb	Jan.–Mar., Nov.– Dec.	Jan., Dec.

Table 1. Continued.				
Family/Species		Habit	Flowering time	Flowering peak
Hypericaceae				
<i>Hypericum brasiliense</i> A. St.-Hil. (218, 508)		shrub	Jan.–May, Dec.	Jan.
<i>Hypericum ternum</i> Choisy (71, 494)		herb	Jan.–Mar., May– Aug., Oct.–Dec.	Jan.–Feb., Nov.–Dec.
Iridaceae				
<i>Alophia geniculata</i> Klatt (376)		herb	Mar.–Apr., Nov.– Dec.	Mar., Nov.
<i>Alophia</i> Herb. sp. indet. 1 (235)		herb	Jan.–Feb.	Jan.
<i>Calydorea campestris</i> (Klatt) Baker (236, 368)		herb	Jan. Mar., Oct.– Dec.	Jan., Nov.–Dec.
<i>Sisyrinchium micranthum</i> Cav. (762)		herb	Jan. Feb., Nov.– Dec.	Nov.–Dec.
<i>Sisyrinchium vaginatum</i> Spreng. (346, 434, 515)		herb	Jan., Mar.–Dec.	May–Oct.
Lamiaceae				
<i>Hyptis lippoides</i> Pohl ex Benth. (399, 423)		herb	July–Oct.	July
<i>Hyptis plectranthoides</i> Benth. (5, 606)		herb	Jan.–May, Oct.– Dec.	Jan., Dec.
<i>Hyptis umbrosa</i> Salzm. ex Benth. (310)		shrub	Jan.–Apr.	Feb.–Mar.
<i>Peltodon radicans</i> Pohl (313, 625)		herb	Mar.–May	Mar.–Apr.
Leguminosae				
<i>Chamaecrista</i> Moench sp. indet. 1 (85)		sub-shrub	Feb.–Mar., Oct.– Dec.	Nov.–Dec.
<i>Crotalaria breviflora</i> DC. (308, 818)		sub-shrub	Jan.–Apr., Dec.	Jan.–Mar.
<i>Lupinus velutinus</i> Benth. (427)		sub-shrub	July–Oct., Dec.	Aug.–Sep.
Lythraceae				
<i>Cuphea glutinosa</i> Cham. & Schltdl. (20)		sub-shrub	Jan. Dec.	Jan., Apr.–June, Aug., Nov.–Dec.
Malpighiaceae				
<i>Byrsonima variabilis</i> A. Juss. (112, 490)		sub-shrub	Jan.–Feb., May, Oct. Dec.	Nov.–Dec.
Malvaceae				
<i>Pavonia kleinii</i> Krapov. & Cristóbal (105)		vine	Jan. Feb., Dec.	Feb.
<i>Sida</i> L. sp. indet. 1 (24, 456)		herb	Jan.–Mar., Oct.– Dec.	Jan., Nov.–Dec.
Melastomataceae				
<i>Leandra erostrata</i> Cogn. (113)		herb	Jan.–Feb., Oct.– Dec.	Jan., Nov.–Dec.
<i>Leandra</i> Raddi sp. indet. 1 (19)		herb	Jan.–Feb., Nov.– Dec.	Jan., Nov.–Dec.
<i>Leandra</i> sp. indet. 2 (401)		shrub	July–Oct.	Aug.–Sep.
<i>Leandra</i> sp. indet. 3 (402)		shrub	July–Dec.	Oct.–Nov.
<i>Microlicia isophylla</i> DC. (103)		sub-shrub	Jan.–Mar., July– Aug., Dec.	Jan.–Feb.
<i>Tibouchina frigidula</i> (DC.) Cogn. (25, 419)		shrub	Jan. Dec.	Jan.–Mar., Dec.
<i>Tibouchina martialis</i> Cogn. (369)		shrub	Apr. June	June
<i>Tibouchina minor</i> Cogn. (32)		herb	Jan. Apr., Dec.	Jan.–Feb.
<i>Trembleya parviflora</i> (D. Don) Cogn. (341, 420)		shrub	Feb. July	June–July
<i>Trembleya phlogiformis</i> DC. (44, 74)		sub-shrub	Jan.–Mar.	Jan.–Mar.
Ochnaceae				
<i>Ouratea semiserrata</i> (Mart. & Nees) Engl. (425)		treelet	June July	June
Orchidaceae				
<i>Epidendrum secundum</i> Jacq. (150)		herb	Jan.–Aug. (f)	Jan., Apr.–May
<i>Habenaria parviflora</i> Lindl. (82, 804)		herb	Jan.–Mar., Dec.	Jan.–Feb.
<i>Oncidium barbaceniae</i> Lindl. (282, 305)		herb	Jan.–Mar., May– Dec.	Jan., May, July, Sep.– Dec.
<i>Oncidium blanchetii</i> Rehb. f. (611)		herb	Jan.–Dec.	July–Nov.
<i>Oncidium</i> Sw. sp. indet. 1 (501)		herb	Jan., Dec.	Jan.

Table 1. Continued.

Family/Species	Habit	Flowering time	Flowering peak
Orobanchaceae			
<i>Esterhazyia macrodonta</i> Cham. & Schltdl. (244)	shrub	Jan., June–Oct.	July–Aug.
Polygalaceae			
<i>Polygala brasiliensis</i> L. (309, 366, 683)	herb	Feb.–Sep., Nov.–Dec.	Mar., June–Aug., Dec.
<i>Polygala cneorum</i> A. St.-Hil. & Moq. (390)	herb	Apr.–Sep., Nov.	May–Aug.
Rubiaceae			
<i>Borreria capitata</i> (Ruiz & Pav.) DC. (322)	herb	Feb.–July	Mar.–Apr.
<i>Borreria tenella</i> Cham. & Schltdl. (192, 667)	herb	Mar.–July	May–June
<i>Declieuxia cordigera</i> var. <i>angustifolia</i> Müll. Arg. (6, 727)	herb	Jan.–Dec.	Jan.–Feb., June, Aug.–Sep.
<i>Galianthe angustifolia</i> (Cham. & Schltdl.) E. L. Cabral (50)	sub-shrub	Jan.–May, July, Sep.–Dec.	Jan.–Feb., Dec.
<i>Galianthe brasiliensis</i> Spreng. (618)	shrub	Jan.–Aug., Oct.–Dec.	Jan.–July, Nov.
<i>Galium hypocarpium</i> (L.) Endl. ex Griseb. (371, 802)	sub-shrub	Jan.–July, Oct.–Dec.	Jan., Apr.–May, Nov.–Dec.
Solanaceae			
<i>Solanum aculeatissimum</i> Jacq. (483)	herb	Jan.–Feb., May, Oct.–Dec.	Jan.–Feb., Oct.–Dec.
<i>Solanum americanum</i> Mill. (488, 675)	herb	Jan., Nov.–Dec.	Nov.
<i>Solanum pseudocapsicum</i> L. (768)	sub-shrub	Jan. Feb., Nov. Dec.	Jan.–Feb., Nov.
<i>Solanum swartzianum</i> Roem. & Schult. (538, 659)	shrub	Jan., Apr.–June, Aug. (f)	Apr.–May
<i>Solanum viarum</i> Dunal (559, 742)	herb	Jan.–Mar., Aug.–Dec.	Feb., Sep., Nov.–Dec.
Verbenaceae			
<i>Verbena hirta</i> Spreng. (31, 243)	sub-shrub	Jan.–Dec.	Jan., Sep.–Dec.
Violaceae			
<i>Viola cerasifolia</i> A. St.-Hil. (124)	herb	Jan.–Feb., Dec.	Jan., Dec.
Xyridaceae			
<i>Xyris asperula</i> Mart. (846)	herb	Feb.–Mar.	Feb.
<i>Xyris tortulla</i> Mart. (2, 350)	herb	Jan.–May, Dec.	Jan.–Mar.

both salverform and spurred flowers. Asteraceae florets were included in the tube type, and their head as a whole was classified as either dish or brush type. Floral measurements with calipers were performed on at least five fresh flowers, each from different plants. The main flower color was determined using a color guidebook (Kornerup & Wanscher, 1963). For our analysis at the community level, the flowers were grouped into six color sets: i. *violet*—showy combinations of blue and red, such as purple and magenta; ii. *pink*—light colors based on blue or red, such as rose, lavender, and lilac; iii. *red*—orange and red; iv. *yellow*—bright and deep yellow; v. *greenish*—colors with sallow tonalities such as greenish, yellowish, or brownish white; and vi. *white*—bright, apparently pure, white. For many species, pollen fertility was estimated by cytoplasmic stainability, using the acetic carmine test (Radford et al., 1974), and stigmatic receptivity was verified with the H₂O₂ catalase

activity test (Zeisler, 1938). In some cases, flowers were tagged and bagged at bud stage, and nectar was extracted on the following day with a graduated microliter syringe (Hamilton, U.S.A.). Nectar volume was registered immediately, and nectar sugar concentration was measured with a hand refractometer (Atago, Japan).

Sexual systems were determined by the presence of both functional anthers and stigmas. Flowers were categorized as either hermaphroditic (monoclinous) or unisexual (diclinous). Plants with unisexual flowers were further classified as monoecious, dioecious, andromonoecious, or gymnomonoecious. Other information about sexual systems—such as the presence of dichogamy and heteromorphy—was noted for some of the species. Spontaneous self-pollination was verified for some species by the report of fruit set in unmanipulated bagged flowers (Kearns & Inouye, 1993). Some pistils were fixed in formaldehyde-

Table 2. Floral features of plant species and their pollination system at the Serra da Bocaina grasslands. In Asteraceae the shape of the blossom (head) and its width are given in parentheses in addition to the tubular florets measurements. Flower size for tube, gullet, bell, and revolver type is effective corolla length vs. opening width; for dish, brush, and inconspicuous type it is the flower width (diameter; d); and for flag type it is keel (k) vs. flag (f) length. Flower symmetry and size for monoecious (U-M) and dioecious (U-D) they plants correspond to female flower first and male flower second, and for gynnomonoecious (GymnM) plants they correspond to hermaphrodite flower first and female flower second. Gynoecium/Androecium = pistil height from the corolla base $\times$ stamen height from the corolla base (or spur base in spurred flowers). Flower measurements are the mode.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color ¹	Color group ¹	Floral resource	Pollination system
Amaryllidaceae									
<i>Hippeastrum glaucescens*</i>	H		tube	Zy, 14 (82) $\times$ 7	114 $\times$ 96	dark red	RE	N	hummingbird
Apiaceae									
<i>Eryngium canaliculatum</i>	H	protandry	incons.	Ac, d1	1 $\times$ 1	yellowish green	GR	N, P	uncertain
<i>Eryngium horridum</i>	H	protandry	incons.	Ac, d1	2 $\times$ 4	yellowish green	GR	N, P	several insect groups
Apocynaceae									
<i>Gonioanthela hilariana</i>	H		dish	Ac, d1	1 $\times$ 1	pale yellow	GR	N	wasp/fly
<i>Mandevilla erecta</i>	H	herkogamy	tube	Ac, 13 $\times$ 3	5 $\times$ 8	pale yellow	GR	N	undet.
<i>Oxypetalum appendiculatum</i>	H		revolver	Ac, 8 $\times$ 3	2 $\times$ 2	greenish lilac	GR	N	wasp/fly
<i>Oxypetalum sublanatum</i>	H		revolver	Ac, 8 $\times$ 5	5 $\times$ 5	pale green	GR	N	bee nectar-flower
<i>Tassadia subulata</i>	H		dish	Ac, d1	1 $\times$ 1	dark ruby	GR	N	syrphid nectar-flower
Aquifoliaceae									
<i>Ilex amara</i>	U-M	temporal dioecism	bell	Ac, 4 $\times$ 2 Ac, 4 $\times$ 2	2 $\times$ $\times$ 2	yellowish white	GR	N N, P?	bee nectar-flower
Asteraceae									
<i>Achyrocline satureioides</i>	GymnM	protandry, 2a	tube (dish)	Ac, 4 $\times$ <1 (14) Ac, 6 $\times$ <1	5 $\times$ 5 10 $\times$	light yellow	GR	N N	wasp/fly
<i>Baccharis aphylla</i>	U-D		tube (dish)	Ac, 5 $\times$ <1 (2) Ac, 4 $\times$ 1 (5)	6 $\times$ $\times$ 6	greenish white	GR	N N	wasp/fly
<i>Baccharis curitybensis</i>	U-D		tube (dish)	Ac, 5 $\times$ <1 (7) Ac, 5 $\times$ <1 (6)	5 $\times$ $\times$ 6	pastel yellow	GR	N N	wasp/fly
<i>Baccharis dracunculifolia</i>	U-D		tube (dish)	Ac, 2 $\times$ <1 (1) Ac, 2 $\times$ <1 (4)	3 $\times$ $\times$ 3	yellowish green	GR	N N, P	wasp/fly
<i>Baccharis intermixta</i>	U-D		tube (dish)	Ac, 2 $\times$ <1 (2) Ac, 3 $\times$ <1 (4)	4 $\times$ $\times$ 4	pale yellow	GR	N N	wasp/fly
<i>Baccharis leptcephala</i>	U-D		tube (dish)	Ac, 2 $\times$ <1 (2) Ac, 3 $\times$ <1 (3)	3 $\times$ $\times$ 4	pale yellow	GR	N N	wasp/fly
<i>Baccharis pentziifolia</i>	U-D		tube (dish)	Ac, 3 $\times$ <1 (2) Ac, 3 $\times$ <1 (4)	5 $\times$ $\times$ 5	yellowish green	GR	N N, P	wasp/fly
<i>Baccharis platypoda</i>	U-D		tube	Ac, 3 $\times$ <1 (5)	7 $\times$	grayish yellow	GR	N	wasp/fly

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, Gynoecium/Androecium size (mm)		Flower color ¹	Color group ¹	Floral resource	Pollination system
			(dish)	Ac, 4 × 1 (6)	× 6			N, P	
<i>Baccharis tarchonanthoides</i>	U-D		tube	Ac, 3 × 1 (7)	4 ×	whitish yellow	GR	N	several insect groups
			(dish)	Ac, 2 × 1 (5)	× 3			N	
<i>Baccharis</i> sp. indet. 1	U-D		tube	Ac, 3 × <1 (2)	7 ×	pale yellow	GR	N	wasp/fly
			(dish)	Ac, 4 × <1 (4)	× 7			N	
<i>Baccharis</i> sp. indet. 2	U-D		tube	Ac, 4 × <1 (2)	5 ×	greenish yellow	GR	N	wasp/fly
			(dish)	Ac, 4 × 1 (6)	× 5			N	
<i>Baccharis</i> sp. indet. 3	U-D		tube	Ac, 2 × <1 (1)	4 ×	pale yellow	GR	N	wasp/fly
			(dish)	Ac, 2 × <1 (2)	× 3			N	
<i>Barrosoa betoniciiiformis</i>	H	protandry, 2a	tube	Ac, 3 × <1 (10)	6 × 5	purple	VI	N	several insect groups
			(brush)						
<i>Campuloclinium</i>	H	protandry, 2a	tube	Ac, 4 × <1 (16)	9 × 8	reddish purple	VI	N	several insect groups
<i>megacephalum</i>			(brush)						
<i>Chaptalia integerrima</i>	GymnM	protandry, 2a	tube	Ac, 10 × 1 (22)	14 × 3	white	WH	N, P	several insect groups
	Ligulate		(brush)	Zy, 2 × <1	3 ×			N	
<i>Chaptalia runcinata</i> var.	GymnM	protandry, 2a	tube	Ac, 3 × <1 (12)	4 × 4	yellow	YE	N, P	several insect groups
<i>graminifolia</i>	Ligulate		(dish)	Zy, 2 × <1	3 ×			N	
<i>Chromolaena</i> cf. <i>decumbens</i>	H	protandry, 2a	tube	Ac, 5 × <1 (9)	7 × 6	reddish violet	VI	N	bee nectar-flower
			(dish)						
<i>Chromolaena xylorrhiza</i>	H	protandry, 2a	tube	Ac, 4 × 1 (4)	6 × 4	purple	VI	N	undet.
			(dish)						
<i>Eremanthus erythropappus</i>	H	protandry, 2a	tube	Ac, 5 × <1 (14)	10 × 8	purple	VI	N, P	several insect groups
			(brush)						
<i>Erigeron maximus</i>	GymnM	protandry, 2a	tube	Ac, 4 × 1 (35)	8 × 7	vivid yellow	YE	N, P	several insect groups
	Ligulate		(dish)	Zy, 3 × <1	7 ×			N	
<i>Eupatorium</i> sp. indet. 1	H	protandry, 2a	tube	Ac, 7 × <1 (10)	15 × 13	white	WH	N, P	bee nectar-flower
			(brush)						
<i>Eupatorium</i> sp. indet. 2	H	protandry, 2a	tube	Ac, 6 × <1 (8)	8 × 7	violet	VI	N	several insect groups
			(dish)						
<i>Eupatorium</i> sp. indet. 3	H	protandry, 2a	tube	Ac, 9 × 1 (12)	19 × 18	purple	VI	N	bee nectar-flower
			(brush)						

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color ¹	Color group ¹	Floral resource	Pollination system
<i>Eupatorium</i> sp. indet. 4	H	protandry, 2a	tube (brush)	Ac, 6 × 1 (8)	9 × 8	white	WH	N, P	several insect groups
<i>Gochnatia paniculata</i>	H	protandry, 2a	tube (brush)	Ac, 3 × <1 (10)	8 × 7	greenish yellow	GR	N, P	wasp/fly
<i>Grazielia gaudichaudiana</i>	H	protandry, 2a	tube (brush)	Ac, 3 × <1 (5)	7 × 5	white	WH	N, P	several insect groups
<i>Hypochaeris gardneri</i>	GymnM Ligulate	protandry, 2a	tube (brush)	Ac, 7 × <1 (16) Zy, 5 × <1	10 × 9 11 ×	vivid yellow	YE	N	bee nectar-flower
<i>Lucilia lycopodioides</i>	GymnM Ligulate	protandry, 2a	tube (dish)	Ac, 6 × 1 (3) Zy, 6 × 1	7 × 6 7 ×	yellowish white	GR	N	wasp/fly
<i>Mikania lundiana</i>	H	protandry, 2a	tube (brush)	Ac, 8 × <1 (4)	11 × 9	yellowish white	GR	N, P	bee nectar-flower
<i>Mikania nummularia</i>	H	protandry, 2a	tube (brush)	Ac, 4 × 1 (3)	5 × 4	white	WH	N	wasp/fly
<i>Mikania sessilifolia</i>	H	protandry, 2a	tube (dish)	Ac, 2 × 1 (5)	4 × 3	yellowish white	GR	N	wasp/fly
<i>Senecio oleosus</i>	GymnM Ligulate	protandry, 2a	tube (brush)	Ac, 7 × 1 (40) Zy, 7 × 1	10 × 9 7 ×	vivid yellow	YE	N, P	syrphid/bee nectar-flower
<i>Stevia myriadenia</i>	H	protandry, 2a	tube (brush)	Ac, 5 × <1 (10)	7 × 6	pink	PK	N, P	several insect groups
<i>Symphyopappus compressus</i>	H	protandry, 2a	tube (brush)	Ac, 6 × 1 (7)	12 × 11	white	WH	N, P	several insect groups
<i>Vernonia herbacea</i>	H	protandry, 2a	tube (brush)	Ac, 5 × <1 (15)	11 × 10	purplish magenta	VI	N	bee nectar-flower
<i>Vernonia megapotamica</i>	H	protandry, 2a	tube (brush)	Ac, 2 × 1 (12)	5 × 4	purple	VI	N, P	several insect groups
<i>Vernonia</i> cf. <i>rosea</i>	H	protandry, 2a	tube (brush)	Ac, 10 × 1 (21)	15 × 14	purple	VI	N	bee nectar-flower
<i>Vernonia tomentella</i>	H	protandry, 2a	tube (brush)	Ac, 9 × <1 (20)	15 × 14	purple	VI	N, P	bee nectar-flower
<i>Vernonia tragiaefolia</i>	H	protandry, 2a	tube (brush)	Zy, 4 × <1 (9)	9 × 7	magenta	VI	N	bee nectar-flower

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color ¹	Color group ¹	Floral resource	Pollination system
<i>Vernonia westiniana</i>	H	protandry, 2a	tube (brush)	Ac, 6 × <1 (11)	10 × 7	reddish purple	VI	N, P	bee nectar-flower
Bromeliaceae									
<i>Dyckia tuberosa</i>	H	herkogamy	tube	Zy, 13 × 5	10 × 12	reddish orange	RE	N	hummingbird
Campanulaceae									
<i>Lobelia camporum</i>	H	protandry, 2a	gullet	Zy, 8 × 3	14 × 12	lilac	PK	N	bee nectar-flower
<i>Wahlenbergia brasiliensis</i>	H	protandry, 2a	bell	Ac, 3 × 3	5 × 4	lilac	PK	N, P	syrphid/bee nectar-flower
Clethraceae									
<i>Clethra scabra</i>	H		bell	Ac, 2 × 2	2 × 2	yellowish white	GR	N	wasp/fly
Convolvulaceae									
<i>Convolvulus crenatifolius</i>	H	heterandry	bell	Ac, 12 × 14	7 × 7, 6	lavender	PK	N P	syrphid/bee nectar-flower
<i>Ipomoea procumbens</i>	H	herkogamy, heterandry	bell	Ac, 38 × 11	26 × 25, 21	pink	PK	N, P	bee nectar-flower
<i>Jacquemontia grandiflora</i>	H	herkogamy	bell	Ac, 18 × 23	14 × 11	violet	VI	N, P?	bee nectar-flower
Cunoniaceae									
<i>Weinmannia organensis</i>	H		dish	Ac, d3	2 × 2	pale yellow	GR	N	several insect groups
Droseraceae									
<i>Drosera montana</i>	H		dish	Ac, d10	3 × 2	pink	PK	P	syrphid/bee pollen-flower
Ericaceae									
<i>Agarista hispidula</i>	H	2a	tube	Ac, 11 × 2	8 × 7	red	RE	N	hummingbird
<i>Gaylussacia chamissonis</i>	H	2a	bell	Ac, 7 × 3	7 × 5	white	WH	N	bee nectar-flower
<i>Gaylussacia jordanensis</i>	H		bell	Ac, 9 × 6	10 × 5	white	WH	N, P	bee nectar-flower
Eriocaulaceae									
<i>Paepalanthus paulensis</i>	U-M		inconsp.	Ac, d1	2 ×	yellowish white	GR	N	several insect groups
			inconsp.	Ac, d1	× 2			N, P	
<i>Paepalanthus polyanthus</i>	U-M		inconsp.	Ac, d1	2 ×	greenish white	GR	N	several insect groups
			inconsp.	Ac, d1	× 2			N, P	
Erythroxylaceae									
<i>Erythroxylum microphyllum</i>	H	heterostyly	dish	Ac, d7	5 × 2, 2 × 5	pastel yellow	GR	N	wasp/fly

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color ¹	Color group ¹	Floral resource	Pollination system
Escalloniaceae									
<i>Escallonia farinacea</i>	H	protandry, herkogamy	bell	Ac, 3 × 2	5 × 4	white	WH	N	bee nectar-flower
Euphorbiaceae									
<i>Croton dichrous</i>	U-M	temporal dioecism	dish dish	Ac, d2 Ac, d3	2 × × 2	yellowish white	GR	N N, P	wasp/fly
Gentianaceae									
<i>Calolisianthus pedunculatus</i>	H	protandry	tube	Zy, 32 × 12	30 × 29	deep red	RE	N?	undet.
<i>Calolisianthus pendulus</i>	H	protandry, protogyny	tube	Zy, 25 × 9	22 × 20	violet	VI	N?	undet.
<i>Deianira nervosa</i>	H	herkogamy, protogyny	dish	Ac, d15	3 × 2	reddish lilac	PK	P	syrphid/bee pollen-flower
<i>Helia oblongifolia</i>	H	protandry	tube	Zy, 20 × 3	16 × 15	yellowish green	GR	N	undet.
<i>Zygostigma australe</i>	H	protogyny	dish	Ac, d20	3 × 2	purple	VI	P?	syrphid/bee pollen-flower
Gesneriaceae									
<i>Sinningia allagophylla</i>	H	protandry, herkogamy	tube	Zy, 14 × 3	11 × 14	reddish orange	RE	N	hummingbird
Hypericaceae									
<i>Hypericum brasiliense</i>	H	apomixis	dish	Ac, d22	4 × 3	vivid yellow	YE	P	syrphid/bee pollen-flower
<i>Hypericum ternum</i>	H	apomixis	dish	Ac, d22	4 × 3	vivid yellow	YE	P?	uncertain
Iridaceae									
<i>Alophia geniculata</i>	H	herkogamy	bell	Ac, 20 × 14	23 × 12	violet	VI	P, N?	bee pollen-flower
<i>Alophia</i> sp. indet. 1	H	herkogamy	bell	Ac, 20 × 12	10 × 8	lilac	PK	P, N?	uncertain
<i>Calydorea campestris</i>	H		dish	Ac, d28	5 × 4	purplish violet	VI	P	syrphid/bee pollen-flower
<i>Sisyrinchium micranthum</i>	H		tube	Ac, 5 × 2	3 × 3	purple	VI	P, O	syrphid/bee pollen-flower
<i>Sisyrinchium vaginatum</i>	H		dish	Ac, d26	6 × 5	vivid yellow	YE	P, O	syrphid/bee pollen-flower
Lamiaceae									
<i>Hyptis lippoides</i>	H	protandry	gullet	Zy, 4 × 2	12 × 8	grayish violet	VI	N	bee nectar-flower
<i>Hyptis plectranthoides</i>	H	protandry	gullet	Zy, 2 × 1	6 × 5	violet	VI	N	bee nectar-flower

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color ¹	Color group ¹	Floral resource	Pollination system
<i>Hyptis umbrosa</i>	H	protandry	gullet	Zy, 3 × 1	5 × 5	violet	VI	N	bee nectar-flower
<i>Peltodon radicans</i>	H	protandry	gullet	Zy, 5 × 1	8 × 6	bluish violet	VI	N	bee nectar-flower
Leguminosae									
<i>Chamaecrista</i> sp. indet. 1	H	herkogamy, heterandry	bell	Zy, 12 × 7	12 × 12, 4	vivid yellow	YE	P	bee pollen-flower
<i>Crotalaria breviflora</i>	H	heterandry, 2a	flag	Zy, k12 × fl2	11 × 10	vivid yellow	YE	N, P	bee nectar-flower
<i>Lupinus velutinus</i>	H	heterandry, 2a	flag	Zy, k13 × fl6	12 × 12	violet	VI	P	bee pollen-flower
Lythraceae									
<i>Cuphea glutinosa</i>	H	protandry	tube	Zy, 8 × 2	9 × 9	purple	VI	N	bee nectar-flower
Malpighiaceae									
<i>Byrsonima variabilis</i>	H		dish	Zy, d13 × 10	3 × 3	vivid yellow	YE	O, P	bee oil-flower
Malvaceae									
<i>Pavonia kleinii</i>	H	herkogamy	bell	Ac, 9 × 9	7 × 6	yellow	YE	N, P	bee nectar-flower
<i>Sida</i> sp. indet. 1	H	herkogamy	bell	Ac, 18 × 25	17 × 9	pastel pink	PK	N	bee nectar-flower
Melastomataceae									
<i>Leandra erostrata</i>	H	apomixis?	dish	Ac, d7	6 × 6	pink	PK	P?	uncertain
<i>Leandra</i> sp. indet. 1	H	apomixis?	dish	Ac, d6	5 × 5	white	WH	P?	uncertain
<i>Leandra</i> sp. indet. 2	H	apomixis?	dish	Ac, d7	14 × 12	pink	PK	P?	uncertain
<i>Leandra</i> sp. indet. 3	H	apomixis?	dish	Ac, d8	15 × 13	pink	PK	P?	uncertain
<i>Microlicia isophylla</i>	H	apomixis?, heterandry	dish	Zy, d20	3 × 4	magenta	VI	P	undet.
<i>Tibouchina frigidula</i>	H	heterandry	dish	Zy, d44	14 × 16	deep violet	VI	P	bee pollen-flower
<i>Tibouchina martialis</i>	H	heterandry	dish	Zy, d55	15 × 20	reddish violet	VI	P	bee pollen-flower
<i>Tibouchina minor</i>	H	heterandry	dish	Zy, d30	6 × 7	violet	VI	P	bee pollen-flower
<i>Trembleya parviflora</i>	H	heterandry	dish	Zy, d18	5 × 5	pink	PK	P	bee pollen-flower
<i>Trembleya phlogiformis</i>	H	heterandry	dish	Zy, d22	4 × 4	purple	VI	P	bee pollen-flower
Ochnaceae									
<i>Ouratea semiserrata</i>	H	protandry	dish	Ac, d16	6 × 5	vivid yellow	YE	P	bee pollen-flower
Orchidaceae									
<i>Epidendrum secundum</i>	H		tube	Zy, 5 × <1	6 × 6	purple	VI	N	undet.
<i>Habenaria parviflora</i>	H		tube, spur	Zy, 8 × <1	9 × 9	grayish green	GR	N	undet.
<i>Oncidium barbaceniae</i>	H		dish	Zy, d22 × 19	3 × 2	vivid yellow	YE	O?	uncertain
<i>Oncidium blanchetii</i>	H		dish	Zy, d24 × 15	2 × 2	vivid yellow	YE	O?	undet.
<i>Oncidium</i> sp. indet. 1	H		dish	Zy, d15 × 11	2 × 2	vivid yellow	YE	O?	undet.

Table 2. Continued.

Family/Species	Sexual system	Floral and reproductive traits	Floral shape	Flower symmetry, size (mm)	Gynoecium/Androecium (mm)	Flower color ¹	Color group ¹	Floral resource	Pollination system
Orobanchaceae									
<i>Esterhazyia macrodonta</i>	H	protandry, herkogamy	gullet	Zy, 24 × 10	38 × 34	reddish orange	RE	N	hummingbird
Polygalaceae									
<i>Polygala brasiliensis</i>	H	protandry?	flag	Zy, k2 × f3	2 × 2	reddish purple	VI	N, P?	bee nectar-flower
<i>Polygala cneorum</i>	H	protandry?	flag	Zy, k3 × f4	3 × 3	grayish magenta	VI	N, P?	bee nectar-flower
Rubiaceae									
<i>Borreria capitata</i>	H	herkogamy, protogyny?	tube	Ac, 3 × 1	4 × 4	white	WH	N	several insect groups
<i>Borreria tenella</i>	H	herkogamy, protogyny	tube	Ac, 2 × 1	3 × 3	purple	VI	N	wasp/fly
<i>Declieuxia cordigera</i> var. <i>angustifolia</i>	H	heterostyly	tube	Ac, 7 × 1	8 × 6, 6 × 8	purple	VI	N	bee nectar-flower
<i>Galianthe angustifolia</i>	H	heterostyly	tube	Ac, 3 × 1	4 × 2, 2 × 4	yellowish white	GR	N	several insect groups
<i>Galianthe brasiliensis</i>	H	heterostyly	tube	Ac, 3 × 1	4 × 3, 3 × 4	white	WH	N	several insect groups
<i>Galium hypocarpium</i>	H		dish	Ac, d1	2 × 1	greenish yellow	GR	N	wasp/fly
Solanaceae									
<i>Solanum aculeatissimum</i>	AndroM		dish	Ac, d12	10 × 8	vivid yellow	YE	P	bee pollen-flower
<i>Solanum americanum</i>	H		dish	Ac, d4	1 × 1	vivid yellow	YE	P	bee pollen-flower
<i>Solanum pseudocapsicum</i>	H		dish	Ac, d11	4 × 3	vivid yellow	YE	P	bee pollen-flower
<i>Solanum swartzianum</i>	H		dish	Ac, d17	5 × 4	vivid yellow	YE	P	bee pollen-flower
<i>Solanum viarum</i>	AndroM		dish	Ac, d16	10 × 8	yellowish green	GR	P	bee pollen-flower
Verbenaceae									
<i>Verbena hirta</i>	H	herkogamy, heterandry	tube	Ac, 6 × 1	3 × 4, 5	purplish violet	VI	N	bee nectar-flower
Violaceae									
<i>Viola cerasifolia</i>	H	herkogamy	tube	Zy, 6 × 3	6 × 4	violet	VI	P, N	bee pollen-flower
Xyridaceae									
<i>Xyris asperula</i>	H		dish	Ac, d13	4 × 4	vivid yellow	YE	P	syrphid/bee pollen-flower
<i>Xyris tortulla</i>	H	herkogamy	dish	Ac, d22	3 × 3	deep yellow	YE	P	syrphid/bee pollen-flower

Abbreviations: Ac = actinomorphic, AndroM = andromonoecious, D = dioecious, GymnM = gymnomonoecious, H = hermaphrodite, inconsp. = inconspicuous, Ligulate = ligulate floret, M = monoecious, N = nectar, O = oil, P = pollen, U = unisexual (diclinous) flower, undet. = undetermined, Zy = zygomorphic, 2a = secondary pollen presentation.

¹ Main color of corolla, except Solanaceae (anthers) and Cunoniaceae (sepals). Color groups: GR = greenish, PK = pink, RE = red, VI = violet, WH = white, YE = yellow.

* Hummingbirds perch on the corolla of the large *Hippeastrum* flowers (corolla tube length in brackets) during visits. Nectar is concealed in a tube at the corolla base, whose size is the effective corolla length.

alcohol-acetic acid (FAA) at 12 to 60 hours after self or cross hand-pollination and analyzed under fluorescence microscopy to observe pollen tube growth (Martin, 1959). Plants along the transects were checked monthly from December 1998 to February 2000, and two phenology parameters were recorded: flowering time—months in which each species was in flower; and the activity blooming peak—months in which more than 50% of the individuals of each species presented flowers (Table 1).

The pollinators for each species were determined through direct observation of flowers for at least four hours (Tables 3, 4). Observation periods were one to two hours, but longer periods (three to eight hours) were necessary for some species with very low frequency of visits; these were usually observed for a total of 12 or more hours (see Table 4). We concentrated our observations on the most probable time of pollinator visitation for each species. Most observation sessions occurred in the middle of the day, because insects are generally more active in this period. The total observation times only include the observations under good climatic conditions and during the flowering peak of each species. To be considered pollinators, visitors had to have pollen grains attached to their bodies and contact the stigmas during their visits. Hummingbirds were identified in the field or through photographs. Insects visiting the flowers were collected, when possible, with an entomological net. Insect specimens were identified by specialists and deposited at MZSP, ZUEC, and MPEG. Non-captured insect visitors were grouped into different hierarchical categories, at least to order and, in a few cases, to genus level (e.g., *Bombus* Latr.). For the broad community study, we categorized captured and non-captured insect visitors into seven functional groups (after Root, 1967, Cummins, 1973): large bees, small bees, wasps, syrphids, other dipterans, butterflies, and beetles (Tables 4, 5). Large bees are those larger than 12 mm (because it is not indigenous to Brazil, *Apis mellifera* was not included in any bee group).

Plant species were divided into nine pollination systems. For those species that were pollinated by one or two functional groups (monophilous and oligophilous; see below), pollination system was based on sets of floral traits common to plants pollinated by each functional group. A second set of species were pollinated by three or more functional groups of which one or two were clearly identified as main pollinators (polyphilous), and pollination system was designated according to the main pollinator. Main pollinators were defined based on pollinator morphology, behavior, and frequency of visits: usually over 60% or 80% of visits for one or two main groups,

respectively; others were designated as secondary pollinators. The final set of species was pollinated by three or more functional groups of apparently similar importance (holophilous) and thus did not have any main pollinator(s). These species were grouped in the pollination system named “several insect groups” (SIG), and their pollinators were designated as indistinct to distinguish them from the secondary and main pollinator categories.

Plant species were classified into four categories representing the degree of specialization/generalization of their interaction with their pollinators: monophily, oligophily, polyphily, and holophily (Table 4). The definition of our first three categories differs from that given by Faegri and van der Pijl (1979), because our unity of reference was functional groups rather than pollinator species. Thus, here, monophily refers to species exclusively pollinated by one functional group. Plant species pollinated by two functional groups (either one or both are their main pollinator[s]) are considered oligophilous. Species pollinated by three or more functional groups are classified either as polyphilous, when one or two groups act as their main pollinators, or holophilous, when there is no preponderance of one or two groups, i.e., when groups act as indistinct pollinators.

RESULTS

We studied a total of 124 species from 35 families (Table 1). Forty species belonged to Asteraceae (32%), followed by Melastomataceae (10 spp., 8%). On the other hand, 16 (46%) and seven (20%) families were represented by only one and two species, respectively.

FLORAL BIOLOGY AND POLLINATOR AGENTS AT THE COMMUNITY LEVEL

A. FLORAL TRAITS

The most common flower color groups were violet (29.8% of the 124 species), greenish (28.2%), and yellow (17.0%). Pink (10.5%), white (9.7%), and red (4.8%) were the least represented groups (Table 2). Most flowers were tubular (47.6%) or dish-shaped (28.2%). Since we considered the shape of the head of Asteraceae as a whole instead of each of its florets, dish-shaped blossoms were the most frequent (43.6%), followed by the brush (16.9%), and tube (15.3%) types. Bell (11.3%), and gullet, inconspicuous, flag, and revolver (12.8% altogether) were the least represented flowers (Table 2). Most plants had either actinomorphic (69.4%) or zygomorphic flowers (25.8%), though a small percentage (4.8%) bore both

Table 3. Pollinator species and the plant species it was collected from or observed pollinating (in the case of hummingbirds) at the Serra da Bocaina grasslands. Pollinators that were seen but not collected are included in Table 4. List of the abbreviations of the plant families: AMA, Amaryllidaceae; API, Apiaceae; APO, Apocynaceae; AQU, Aquifoliaceae; AST, Asteraceae; BRO, Bromeliaceae; CAM, Campanulaceae; CLE, Clethraceae; CON, Convolvulaceae; CUN, Cunoniaceae; DRO, Droseraceae; ERIC, Ericaceae; ERIO, Eriocaulaceae; ERY, Erythroxylaceae; ESC, Escalloniaceae; EUP, Euphorbiaceae; GEN, Gentianaceae; GES, Gesneriaceae; HYP, Hypericaceae; IRI, Iridaceae; LAM, Lamiaceae; LEG, Leguminosae; LYT, Lythraceae; MALP, Malpighiaceae; MALV, Malvaceae; MEL, Melastomataceae; OCH, Ochnaceae; ORC, Orchidaceae; ORO, Orobanchaceae; POL, Polygalaceae; RUB, Rubiaceae; SOL, Solanaceae; VER, Verbenaceae; VIO, Violaceae; XYR, Xyridaceae.

Pollinator family and species	Plant family	Plant species
Trochiliformes		
Trochilidae (hummingbirds)		
<i>Chlorostilbon aureoventris berlepschi</i> Pinto	ERIC:	<i>Agarista hispidula</i>
<i>Clytolaema rubricauda</i> (Boddaert)	GES:	<i>Sinningia allagophylla</i>
<i>Colibri serrirostris</i> (Vieillot)	BRO:	<i>Dyckia tuberosa</i>
	GES:	<i>Sinningia allagophylla</i>
<i>Leucochloris albicollis</i> (Vieillot)	AMA:	<i>Hippeastrum glaucescens</i>
	ERIC:	<i>Agarista hispidula</i>
	GES:	<i>Sinningia allagophylla</i>
	ORO:	<i>Esterhazyia macrodonta</i>
<i>Stephanoxis lalandi lalandi</i> (Vieillot)	GES:	<i>Sinningia allagophylla</i>
Coleoptera (beetles)		
Buprestidae (jewel beetles)		
<i>Conognatha</i> Cobos sp. indet. 1	ERIO:	<i>Paepalanthus paulensis</i>
Cantharidae (soldier beetles)		
<i>Discodon tucumanum</i> Pic	ERIO:	<i>Paepalanthus paulensis</i>
Cantharidae sp. indet. 1	API:	<i>Eryngium canaliculatum</i>
	AST:	<i>Baccharis pentziifolia</i> , <i>Baccharis tarchonanthoides</i> , <i>Barrosoa betoniciiiformis</i> , <i>Campuloclinium megacephalum</i> , <i>Chaptalia integerrima</i> , <i>Erigeron maximus</i> , <i>Eupatorium</i> sp. indet. 2, <i>Grazielia gaudichaudiana</i>
Cantharidae sp. indet. 2	ERIO:	<i>Paepalanthus polyanthus</i>
	CLE:	<i>Clethra scabra</i>
	CUN:	<i>Weinmannia organensis</i>
Cerambycidae (longhorn beetles)		
<i>Rhinotragus festivus</i> Perty	CLE:	<i>Clethra scabra</i>
Elateridae (click beetles)		
<i>Cardiorhinus</i> Eschscholtz sp. indet. 1	API:	<i>Eryngium canaliculatum</i>
Melyridae (softwinged flower beetles)		
<i>Astylus sexmaculatus</i> Perty	AST:	<i>Eupatorium</i> sp. indet. 4
Diptera (flies)		
Bombyliidae (beeflies)		
<i>Euprepina</i> Hull sp. indet. 1	AST:	<i>Campuloclinium megacephalum</i>
<i>Exoprosopa</i> Macquart sp. indet. 1	RUB:	<i>Borreria capitata</i>
<i>Paravilla</i> Painter sp. indet. 1	AST:	<i>Campuloclinium megacephalum</i> , <i>Chaptalia runcinata</i> , <i>Stevia myriadenia</i> , <i>Vernonia megapotamica</i>
Culicidae (biting flies)		
Culicidae sp. indet. 1	API:	<i>Eryngium horridum</i>
Curtonotidae (curtonotid flies)		
Curtonotidae sp. indet. 1	API:	<i>Eryngium horridum</i>
	AST:	<i>Baccharis platypoda</i> , <i>Mikania sessilifolia</i>
Curtonotidae sp. indet. 2	RUB:	<i>Galianthe angustifolia</i>
Sarcophagidae (flesh flies)		
Sarcophagidae sp. indet. 1	RUB:	<i>Galianthe angustifolia</i>
Sarcophagidae sp. indet. 2	ERIO:	<i>Paepalanthus paulensis</i>

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
Sciaridae (sciarid flies)		
Sciaridae sp. indet. 1	AST:	<i>Baccharis aphylla</i> , <i>Baccharis tarchonanthoides</i>
	ERIO:	<i>Paepalanthus paulensis</i>
Syrphidae (hover-flies)		
<i>Allograpta exotica</i> (Wiedemann)	CAM:	<i>Wahlenbergia brasiliensis</i>
	GEN:	<i>Zygostigma australe</i>
	IRI:	<i>Alophia</i> sp. indet. 1, <i>Sisyrinchium micranthum</i>
	RUB:	<i>Galianthe angustifolia</i>
<i>Palpada rufipedes</i> Thompson	APO:	<i>Tassadia subulata</i>
<i>Pseudodoros clavatus</i> (Fabricius)	RUB:	<i>Borreria capitata</i> , <i>Galianthe brasiliensis</i>
<i>Syrphus phaeostigma</i> Wiedemann	AST:	<i>Baccharis leptcephala</i>
<i>Toxomerus watsoni</i> (Curran)	APO:	<i>Tassadia subulata</i>
	AST:	<i>Achyrocline satureioides</i> , <i>Baccharis leptcephala</i> , <i>Baccharis pentziifolia</i> , <i>Baccharis tarchonanthoides</i> , <i>Chaptalia runcinata</i> , <i>Gochnatia paniculata</i> , <i>Mikania sessilifolia</i> , <i>Senecio oleosus</i>
	CAM:	<i>Wahlenbergia brasiliensis</i>
	DRO:	<i>Drosera montana</i>
	ERIO:	<i>Paepalanthus paulensis</i> , <i>Paepalanthus polyanthus</i>
	EUP:	<i>Croton dichrous</i>
	IRI:	<i>Alophia geniculata</i> , <i>Sisyrinchium vaginatum</i>
	LYT:	<i>Cuphea glutinosa</i>
	RUB:	<i>Borreria capitata</i> , <i>Galianthe brasiliensis</i>
	XYR:	<i>Xyris asperula</i> , <i>Xyris tortulla</i>
<i>Toxomerus</i> Macquart sp. indet. 1	APO:	<i>Tassadia subulata</i>
	AST:	<i>Achyrocline satureioides</i> , <i>Chaptalia runcinata</i>
	ERIO:	<i>Paepalanthus paulensis</i>
	IRI:	<i>Sisyrinchium vaginatum</i>
	RUB:	<i>Borreria capitata</i>
Syrphidae sp. indet. 1	DRO:	<i>Drosera montana</i>
	XYR:	<i>Xyris asperula</i>
Syrphidae sp. indet. 2	IRI:	<i>Alophia geniculata</i>
Syrphidae sp. indet. 3	AST:	<i>Baccharis pentziifolia</i>
Syrphidae sp. indet. 4	XYR:	<i>Xyris tortulla</i>
Syrphidae sp. indet. 5	AST:	<i>Mikania sessilifolia</i> , <i>Stevia myriadenia</i>
	GEN:	<i>Deianira nervosa</i>
	IRI:	<i>Calydorea campestris</i>
Syrphidae sp. indet. 6	AST:	<i>Chaptalia runcinata</i>
Tachinidae (tachinid flies)		
<i>Cylindromyia dorsalis</i> (Wiedemann)	AST:	<i>Grazielia gaudichaudiana</i>
	HYPERIC:	<i>Hypericum brasiliense</i>
<i>Jurinella</i> cf. <i>corpulenta</i> (Townsend)	API:	<i>Eryngium horridum</i>
	AST:	<i>Baccharis dracunculifolia</i> , <i>Baccharis platypoda</i> , <i>Mikania sessilifolia</i>
Tachinidae sp. indet. 1	AST:	<i>Eupatorium</i> sp. indet. 2
	RUB:	<i>Galianthe brasiliensis</i>
Tachinidae sp. indet. 2	CLE:	<i>Clethra scabra</i>
Tachinidae sp. indet. 3	ERIO:	<i>Paepalanthus paulensis</i>
Tachinidae sp. indet. 4	AST:	<i>Baccharis</i> sp. indet. 2
	RUB:	<i>Galianthe brasiliensis</i>
Tachinidae sp. indet. 5	AST:	<i>Eremanthus erythropappus</i>
Tachinidae sp. indet. 6	AST:	<i>Vernonia westiniana</i>
Tachinidae sp. indet. 7	RUB:	<i>Galianthe angustifolia</i>
Tachinidae sp. indet. 8	AST:	<i>Achyrocline satureioides</i> , <i>Baccharis dracunculifolia</i> , <i>Symphopappus compressus</i>
Tachinidae sp. indet. 9	API:	<i>Eryngium horridum</i>
Tephritidae (fruit flies)		
<i>Trupanea</i> Schrank sp. indet. 1	RUB:	<i>Galium hypocarpium</i>

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
Family indet. (flies)		
Diptera sp. indet. 1	API:	<i>Eryngium horridum</i>
Diptera sp. indet. 2	AST:	<i>Chaptalia runcinata</i>
Diptera sp. indet. 3	AST:	<i>Chaptalia runcinata</i>
Diptera sp. indet. 4	AST:	<i>Baccharis dracunculifolia</i>
Diptera sp. indet. 5	ERIO:	<i>Paepalanthus polyanthus</i>
Diptera sp. indet. 6	AST:	<i>Erigeron maximus</i>
Diptera sp. indet. 7	CLE:	<i>Clethra scabra</i>
Diptera sp. indet. 8	ERIO:	<i>Paepalanthus polyanthus</i>
Hymenoptera		
Andrenidae, Panurginae (dagger bees)		
<i>Anthrenoides</i> Ducke sp. indet. 1	VIO:	<i>Viola cerasifolia</i>
Apidae, Apini (honey bees)		
<i>Apis mellifera</i> Linnaeus	AQU:	<i>Ilex amara</i>
	AST:	<i>Baccharis dracunculifolia</i> , <i>Baccharis pentziifolia</i> , <i>Baccharis platypoda</i> , <i>Baccharis</i> sp. indet. 2, <i>Barrosoa betoniciiiformis</i> , <i>Campuloclinium megacephalum</i> , <i>Eremanthus erythropappus</i> , <i>Eupatorium</i> sp. indet. 2, <i>Grazielia gaudichaudiana</i> , <i>Hypochaeris gardneri</i> , <i>Mikania lundiana</i> , <i>Stevia myriadenia</i> , <i>Symphyopappus compressus</i> , <i>Vernonia westiniana</i>
	CAM:	<i>Wahlenbergia brasiliensis</i>
	CLE:	<i>Clethra scabra</i>
	CON:	<i>Convolvulus crenatifolius</i>
	ERIC:	<i>Gaylussacia chamissonis</i> , <i>Gaylussacia jordanensis</i>
	EUP:	<i>Croton dichrous</i>
	IRE:	<i>Sisyrinchium vaginatum</i>
	LAM:	<i>Hyptis lippoides</i> , <i>Hyptis plectranthoides</i> , <i>Hyptis umbrosa</i> , <i>Peltodon radicans</i>
	LYT:	<i>Cuphea glutinosa</i>
	RUB:	<i>Borreria capitata</i> , <i>Galianthe angustifolia</i> , <i>Galianthe brasiliensis</i>
	VER:	<i>Verbena hirta</i>
Apidae, Bombini (bumblebees)		
<i>Bombus atratus</i> Franklin	APO:	<i>Oxypetalum sublanatum</i>
	AST:	<i>Campuloclinium megacephalum</i> , <i>Chromolaena</i> cf. <i>decumbens</i> , <i>Steria myriadenia</i> , <i>Symphyopappus compressus</i> , <i>Vernonia tomentella</i> , <i>Vernonia westiniana</i>
	CAM:	<i>Lobelia camporum</i>
	CON:	<i>Ipomoea procumbens</i> , <i>Jacquemontia grandiflora</i>
	IRE:	<i>Alophia geniculata</i>
	LAM:	<i>Hyptis lippoides</i> , <i>Hyptis plectranthoides</i>
	LEG:	<i>Crotalaria breviflora</i> , <i>Lupinus velutinus</i>
	LYT:	<i>Cuphea glutinosa</i>
	MEL:	<i>Tibouchina frigidula</i> , <i>Tibouchina minor</i> , <i>Trembleya phlogiformis</i>
	RUB:	<i>Declieuxia cordigera</i> , <i>Galianthe angustifolia</i>
	VER:	<i>Verbena hirta</i>
<i>Bombus brasiliensis</i> Lepeletier	AST:	<i>Stevia myriadenia</i> , <i>Vernonia westiniana</i>
	LEG:	<i>Crotalaria breviflora</i>
	LYT:	<i>Cuphea glutinosa</i>
	VER:	<i>Verbena hirta</i>
<i>Bombus morio</i> (Swederus)	AST:	<i>Vernonia westiniana</i>
	LYT:	<i>Cuphea glutinosa</i>
	RUB:	<i>Galianthe angustifolia</i>
	VER:	<i>Verbena hirta</i>
Apidae, Centridini (digger bees)		
<i>Centris burgdorfi</i> Friese	CAM:	<i>Lobelia camporum</i>
	RUB:	<i>Declieuxia cordigera</i>

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
<i>Centris discolor</i> Smith	MALP:	<i>Byrsonima variabilis</i>
	MEL:	<i>Tibouchina frigidula</i>
<i>Centris</i> cf. <i>insularis</i> Smith	MALP:	<i>Byrsonima variabilis</i>
<i>Centris klugi</i> Friese	AST:	<i>Hypochoeris gardneri</i> , <i>Vernonia</i> cf. <i>rosea</i> , <i>Vernonia tomentella</i>
	LEG:	<i>Chaemaecrista</i> sp. indet. 1
	LYT:	<i>Cuphea glutinosa</i>
	MALP:	<i>Byrsonima variabilis</i>
	MEL:	<i>Tibouchina minor</i>
<i>Centris tarsata</i> Smith	MALP:	<i>Byrsonima variabilis</i>
	VER:	<i>Verbena hirta</i>
<i>Centris</i> (<i>Melacentris</i>) Moure sp. indet. 1	MALP:	<i>Byrsonima variabilis</i>
Apidae, Ceratinini (dwarf carpenter bees)		
<i>Ceratina</i> cf. <i>asuncionis</i> Strand	AST:	<i>Senecio oleosus</i> , <i>Vernonia herbacea</i> , <i>Vernonia tomentella</i>
	CAM:	<i>Lobelia camporum</i>
	MALV:	<i>Sida</i> sp. indet. 1
	VER:	<i>Verbena hirta</i>
<i>Ceratina</i> Latreille sp. indet. 1	LYT:	<i>Cuphea glutinosa</i>
<i>Ceratina</i> sp. indet. 2	CON:	<i>Convolvulus crenatifolius</i>
Apidae, Erieroacidini		
<i>Mesonychium caerulescens</i> Lepeletier & Serville	AST:	<i>Vernonia tomentella</i>
	LYT:	<i>Cuphea glutinosa</i>
	RUB:	<i>Galianthe angustifolia</i>
	VER:	<i>Verbena hirta</i>
Apidae, Eucerini (long-horned bees)		
<i>Gaesischia nigra</i> Moure	AST:	<i>Vernonia tragiaefolia</i>
<i>Melissoptila aureocincta</i> Urban	AST:	<i>Symphyopappus compressus</i>
Apidae, Meliponini (stingless bees)		
<i>Melipona bicolor bicolor</i> Lepeletier	AST:	<i>Eremanthus erythropappus</i> , <i>Eupatorium</i> sp. indet. 3, <i>Grazielia gaudichaudeana</i> , <i>Mikania lundiana</i> , <i>Vernonia megapotamica</i> , <i>Vernonia tomentella</i> , <i>Vernonia westiniana</i>
	CLE:	<i>Clethra scabra</i>
	ERIC:	<i>Gaylussacia chamissonis</i>
	IRI:	<i>Alophia geniculata</i>
	LAM:	<i>Hyptis lippiioides</i>
	MEL:	<i>Trembleya parviflora</i>
	OCH:	<i>Ouratea semiserrata</i>
<i>Melipona quadrifasciata anthidioides</i> (Lepeletier)	AST:	<i>Campuloclinium megacephalum</i> , <i>Eremanthus erythropappus</i> , <i>Mikania lundiana</i> , <i>Symphyopappus compressus</i>
<i>Paratrigona subnuda</i> Moure	AST:	<i>Chaptalia integerrima</i> , <i>Eremanthus erythropappus</i> , <i>Mikania lundiana</i>
<i>Plebeia droryana</i> (Friese)	AST:	<i>Achyrocline satureioides</i>
<i>Plebeia saiqui</i> (Friese)	API:	<i>Eryngium horridum</i>
	AQU:	<i>Ilex amara</i>
	AST:	<i>Vernonia westiniana</i>
	ERI:	<i>Gaylussacia jordanensis</i>
	IRI:	<i>Alophia geniculata</i> , <i>Calydorea campestris</i>
	LAM:	<i>Hyptis lippiioides</i>
	MALP:	<i>Byrsonima variabilis</i>
<i>Scaptotrigona bipunctata</i> (Lepeletier)	CLE:	<i>Clethra scabra</i>
<i>Schwarziana quadripunctata</i> (Lepeletier)	AST:	<i>Baccharis</i> sp. indet. 2, <i>Eremanthus erythropappus</i> , <i>Eupatorium</i> sp. indet. 4, <i>Grazielia gaudichaudeana</i> , <i>Mikania lundiana</i>
	CLE:	<i>Clethra scabra</i>
	HYP:	<i>Hypericum brasiliense</i>

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
<i>Trigona spinipes</i> (Fabricius)	AST: ERIO: LAM:	<i>Baccharis</i> sp. indet. 2 <i>Paepalanthus paulensis</i> <i>Hyptis lippoides</i>
Apidae, Tapinotaspidini (digger bees)		
<i>Monoeca</i> Lepeletier & Serville sp. indet. 1	MALP:	<i>Byrsonima variabilis</i>
<i>Paratetrapedia (Lophopedia)</i> cf. <i>pygmaea</i> (Schrottky)	AST:	<i>Stevia myriadenia</i>
<i>Paratetrapedia (Xanthopedia)</i> Michener & Moure sp. indet. 1	XYR: MALP:	<i>Xyris tortulla</i> <i>Byrsonima variabilis</i>
<i>Paratetrapedia (Trigonopedia)</i> Moure sp. indet. 1	AST:	<i>Stevia myriadenia</i>
Apidae, Xylocopini (giant carpenter bees)		
<i>Xylocopa brasilianorum</i> (Linnaeus)	AST: CON: MEL: VER:	<i>Symphiopappus compressus</i> <i>Ipomoea procumbens</i> <i>Tibouchina frigidula</i> , <i>Tibouchina martialis</i> <i>Verbena hirta</i>
Braconidae (braconid wasps)		
Braconidae sp. indet. 1	AST:	<i>Baccharis platypoda</i>
Chrysididae (cuckoo wasps)		
Chrysididae sp. indet. 1	AST:	<i>Baccharis dracunculifolia</i>
Colletidae, Colletini (plasterer bees)		
<i>Colletes</i> Latreille sp. indet. 1	AST: ESC:	<i>Hypochaeris gardneri</i> <i>Escallonia farinacea</i>
Eurytomidae (eurytomid wasps)		
Eurytomidae sp. indet. 1	RUB:	<i>Galium hypocarpium</i>
Gasteruptiidae (gasteruptid wasps)		
Gasteruptiinae sp. indet. 1	EUP:	<i>Croton dichrous</i>
Halictidae, Augochlorini (sweat bees)		
<i>Augochlorodes turrifaciens</i> Moure	VIO:	<i>Viola cerasifolia</i>
<i>Augochloropsis</i> cf. <i>cognata</i> Moure	AQU: AST: CLE: EUP: IRI: LAM: MALP: MALV: RUB:	<i>Ilex amara</i> <i>Campuloclinium megacephalum</i> , <i>Vernonia tomentella</i> <i>Clethra scabra</i> <i>Croton dichrous</i> <i>Calydorea campestris</i> <i>Hyptis lippoides</i> <i>Byrsonima variabilis</i> <i>Pavonia kleinii</i> <i>Borreria capitata</i> , <i>Galianthe brasiliensis</i>
<i>Augochloropsis cyanea</i> (Schrottky)	AST: ERIC: EUP: LYT: RUB: SOL: XYR:	<i>Barrosoa betoniciiformis</i> , <i>Campuloclinium megacephalum</i> , <i>Chaptalia runcinata</i> , <i>Eupatorium</i> sp. indet. 4, <i>Grazielia gaudichaudiana</i> , <i>Vernonia tomentella</i> <i>Gaylussacia jordanensis</i> <i>Croton dichrous</i> <i>Cuphea glutinosa</i> <i>Galianthe angustifolia</i> , <i>Galianthe brasiliensis</i> <i>Solanum aculeatissimum</i> , <i>Solanum pseudocapsicum</i> , <i>Solanum swartzianum</i> , <i>Solanum viarum</i> <i>Xyris asperula</i>
<i>Augochloropsis iris</i> (Schrottky)	AST: IRE:	<i>Campuloclinium megacephalum</i> <i>Alophia geniculata</i>
<i>Augochloropsis</i> Cockerell sp. indet. 1	AST:	<i>Eupatorium</i> sp. indet. 2, <i>Stevia myriadenia</i>

Table 3. Continued.		
Pollinator family and species	Plant family	Plant species
<i>Ceratalictus</i> Moure sp. indet. 1	ERIC:	<i>Gaylussacia chamissonis</i> , <i>Gaylussacia jordanensis</i>
	LAM:	<i>Hyptis umbrosa</i>
	LYT:	<i>Cuphea glutinosa</i>
	MEL:	<i>Trembleya phlogiformis</i>
	POL:	<i>Polygala cneorum</i>
	RUB:	<i>Galianthe brasiliensis</i>
	SOL:	<i>Solanum pseudocapsicum</i>
	AQU:	<i>Ilex amara</i>
	AST:	<i>Vernonia westiniana</i>
	ERIC:	<i>Gaylussacia jordanensis</i>
	ERY:	<i>Erythroxylum microphyllum</i>
	GEN:	<i>Zygostigma australe</i>
	IRI:	<i>Alophia</i> sp. indet. 1
	LAM:	<i>Hyptis lippoides</i> , <i>Hyptis plectranthoides</i> , <i>Hyptis umbrosa</i>
	RUB:	<i>Borreria capitata</i> , <i>Borreria tenella</i> , <i>Galianthe brasiliensis</i>
<i>Paroxystoglossa</i> cf. <i>jocasta</i> (Schrottky)	IRI:	<i>Alophia geniculata</i>
<i>Paroxystoglossa</i> Moure sp. indet. 1	AST:	<i>Chaptalia integerrima</i>
<i>Pseudaugochlora</i> cf. <i>graminea</i> (Fabricius)	VER:	<i>Verbena hirta</i>
Augochlorini sp. indet. 1	RUB:	<i>Declieuxia cordigera</i>
Halictidae, Halictini (sweat bees)		
<i>Agapostemon</i> Guerin-Meneville sp. indet. 1	AST:	<i>Symphyopappus compressus</i>
<i>Dialictus</i> Robertson sp. indet. 1	ERIC:	<i>Gaylussacia jordanensis</i>
	IRI:	<i>Alophia geniculata</i> , <i>Calydorea campestris</i> , <i>Sisyrinchium micranthum</i>
	OCH:	<i>Ouratea semiserrata</i>
<i>Dialictus</i> sp. indet. 2	VIO:	<i>Viola cerasifolia</i>
<i>Pseudagapostemon cyaneus</i> Moure & Sakagami	AST:	<i>Chaptalia runcinata</i>
	AST:	<i>Mikania lundiana</i> , <i>Senecio oleosus</i>
Halictini sp. indet. 1	HYP:	<i>Hypericum brasiliense</i>
Halictini sp. indet. 2	IRI:	<i>Alophia geniculata</i>
	VER:	<i>Verbena hirta</i>
Leucospidae (leucospid wasps)		
Leucospidae sp. indet. 1	AST:	<i>Baccharis intermixta</i>
Megachilidae, Anthidiini (mason and carder bees)		
<i>Anthidium sertanicola</i> Moure & Urban	LEG:	<i>Crotalaria breviflora</i>
	LYT:	<i>Cuphea glutinosa</i>
<i>Epanthidium autumnale</i> (Schrottky)	AST:	<i>Stevia myriadenia</i>
Megachilidae, Megachilini (leaf- cutter, mason and cuckoo bees)		
<i>Coelioxys</i> Latreille sp. indet. 1	AST:	<i>Erigeron maximus</i> , <i>Senecio oleosus</i>
<i>Coelioxys</i> sp. indet. 2	AST:	<i>Stevia myriadenia</i>
<i>Megachile</i> cf. <i>anthidioides</i> Radoskowski	AST:	<i>Symphyopappus compressus</i>
	LYT:	<i>Cuphea glutinosa</i>
<i>Megachile iheringi</i> Schrottky	AST:	<i>Eupatorium</i> sp. indet. 1, <i>Vernonia tomentella</i>
	ERIC:	<i>Gaylussacia jordanensis</i>
	HYP:	<i>Hypericum brasiliense</i>
	LEG:	<i>Lupinus velutinus</i>
<i>Megachile laeta</i> Smith	LEG:	<i>Lupinus velutinus</i>
	VER:	<i>Verbena hirta</i>

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
<i>Megachile terrestris</i> Schrottky	AST:	<i>Eupatorium</i> sp. indet. 1, <i>Vernonia tomentella</i>
Pompilidae (spider wasps)		
Pompilidae sp. indet. 1	AST:	<i>Baccharis</i> sp. indet. 2
Pompilidae sp. indet. 2	AST:	<i>Baccharis platypoda</i>
Pompilidae sp. indet. 3	AST:	<i>Baccharis</i> sp. indet. 2
Pompilidae sp. indet. 1	AST:	<i>Baccharis</i> sp. indet. 2
Scoliidae (digger wasps)		
Scoliidae sp. indet. 1	AST:	<i>Symphypappus compressus</i> , <i>Vernonia westiniana</i>
Sphecidae (mud-dauber and sphecid wasps)		
<i>Bicyrtes paranae</i> Bohart	RUB:	<i>Galianthe angustifolia</i>
<i>Pryonyx thomaz</i> (Fabricius)	AST:	<i>Baccharis dracunculifolia</i>
<i>Sphex dorsalis</i> Lepeletier	RUB:	<i>Galianthe angustifolia</i>
<i>Sphex opacus</i> Dahlbom	AST:	<i>Eupatorium</i> sp. indet. 4
Cercerini sp. indet. 1	CLE:	<i>Clethra scabra</i>
Cercerini sp. indet. 2	AST:	<i>Mikania nummularia</i>
	CLE:	<i>Clethra scabra</i>
Larrinae sp. indet. 1	AST:	<i>Achyrocline satureioides</i>
Tenthredinidae (sawflies)		
Tenthredinidae sp. indet. 1	RUB:	<i>Galianthe brasiliensis</i>
Tiphiidae (tiphiid wasps)		
Tiphiidae sp. indet. 1	AST:	<i>Baccharis</i> sp. indet. 2
Vespidae (paper wasps)		
<i>Agelaia vicina</i> (Saussure)	AST:	<i>Baccharis intermixta</i>
	ERIO:	<i>Paepalanthus polyanthus</i>
<i>Brachygastra lecheguana</i> (Latreille)	AST:	<i>Baccharis</i> sp. indet. 3
<i>Mischocyttarus drewseni</i> Saussure	AQU:	<i>Ilex amara</i>
	AST:	<i>Achyrocline satureioides</i> , <i>Baccharis aphylla</i> , <i>Baccharis dracunculifolia</i> , <i>Baccharis pentziifolia</i> , <i>Baccharis</i> sp. indet. 2, <i>Chaptalia integerrima</i> , <i>Eupatorium</i> sp. indet. 4, <i>Gochnatia paniculata</i>
	CLE:	<i>Clethra scabra</i>
	ERY:	<i>Erythroxylum microphyllum</i>
	EUP:	<i>Croton dichrous</i>
	RUB:	<i>Galianthe brasiliensis</i>
<i>Polistes billardieri</i> Fabricius	AQU:	<i>Ilex amara</i>
	AST:	<i>Achyrocline satureioides</i> , <i>Baccharis</i> sp. indet. 2, <i>Baccharis</i> sp. indet. 3, <i>Gochnatia paniculata</i> , <i>Mikania sessilifolia</i>
	ERY:	<i>Erythroxylum microphyllum</i>
	RUB:	<i>Galianthe brasiliensis</i>
<i>Polistes cinerascens</i> Saussure	APO:	<i>Gonioanthela hilariana</i>
	AST:	<i>Baccharis dracunculifolia</i> , <i>Baccharis platypoda</i>
<i>Polybia fastidiosuscula</i> Saussure	AST:	<i>Baccharis platypoda</i> , <i>Baccharis</i> sp. indet. 2
	CLE:	<i>Clethra scabra</i>
	RUB:	<i>Galianthe angustifolia</i>
<i>Polybia minarum</i> Ducke	CLE:	<i>Clethra scabra</i>
	CUN:	<i>Weinmannia organensis</i>
<i>Polybia scutellaris</i> (White)	AST:	<i>Baccharis tarchonanthoides</i>
	EUP:	<i>Croton dichrous</i>
<i>Polybia sericea</i> (Olivier)	APO:	<i>Gonioanthela hilariana</i> , <i>Oxypetalum appendiculatum</i>
	RUB:	<i>Borreria tenella</i>
<i>Protonectarina sylveirae</i> (Saussure)	AST:	<i>Baccharis curitybensis</i>
<i>Protopolybia sedula</i> (Saussure)	AST:	<i>Baccharis</i> sp. indet. 2
<i>Synoecca cyanea</i> (Fabricius)	CLE:	<i>Clethra scabra</i>
Family indet. (wasps)		
Hymenoptera sp. indet. 1	AST:	<i>Achyrocline satureioides</i> , <i>Mikania nummularia</i>
Hymenoptera sp. indet. 2	AST:	<i>Lucilia lycopodioides</i> , <i>Mikania nummularia</i>

Table 3. Continued.

Pollinator family and species	Plant family	Plant species
	ERY:	<i>Erythroxylum microphyllum</i>
	RUB:	<i>Borreria capitata</i> , <i>Borreria tenella</i>
Hymenoptera sp. indet. 3	AST:	<i>Mikania sessilifolia</i>
	LYT:	<i>Cuphea glutinosa</i>
Hymenoptera sp. indet. 4	AST:	<i>Baccharis aphylla</i>
Hymenoptera sp. indet. 5	AST:	<i>Baccharis pentziifolia</i>
Hymenoptera sp. indet. 6	AST:	<i>Eupatorium</i> sp. indet. 2
Hymenoptera sp. indet. 7	AST:	<i>Achyrocline satureioides</i>
Hymenoptera sp. indet. 8	AST:	<i>Achyrocline satureioides</i>
Hymenoptera sp. indet. 9	AST:	<i>Achyrocline satureioides</i>
Hymenoptera sp. indet. 10	AST:	<i>Baccharis pentziifolia</i>
	CLE:	<i>Clethra scabra</i>
Hymenoptera sp. indet. 11	LYT:	<i>Cuphea glutinosa</i>
Hymenoptera sp. indet. 12	RUB:	<i>Galianthe brasiliensis</i>
Hymenoptera sp. indet. 13	AST:	<i>Grazielia gaudichaudiana</i>
Hymenoptera sp. indet. 14	AST:	<i>Baccharis dracunculifolia</i>
Hymenoptera sp. indet. 15	RUB:	<i>Galianthe angustifolia</i>
Lepidoptera (butterflies)		
Hesperiidae (skippers and darters)		
<i>Sarbia</i> cf. <i>damippe</i> (Mabille & Boulet)	AST:	<i>Barrosoa betoniciiiformis</i> , <i>Campuloclinium megacephalum</i>
<i>Sarbia</i> cf. <i>xanthippe</i> (Latreille)	AST:	<i>Vernonia westiniana</i>
<i>Thespies</i> Godman sp. indet. 1	AST:	<i>Campuloclinium megacephalum</i>
<i>Urbanus</i> Hübner sp. indet. 1	VER:	<i>Verbena hirta</i>
Hesperiinae sp. indet. 1	AST:	<i>Grazielia gaudichaudiana</i>
Pyrrhopyginae sp. indet. 1	AST:	<i>Chaptalia integerrima</i> , <i>Vernonia westiniana</i>
Lycaenidae (coppers and hair streaks)		
<i>Thecla</i> Fabricius sp. indet. 1	AST:	<i>Chaptalia runcinata</i> , <i>Mikania nummularia</i> , <i>Vernonia westiniana</i>
	RUB:	<i>Galianthe brasiliensis</i>
Riodininae sp. indet. 1	API:	<i>Eryngium horridum</i>
Nymphalidae (danais and browns)		
<i>Agraulis vanillae maculosa</i> (Stichel)	AST:	<i>Vernonia megapotamica</i>
<i>Vanessa myrinna</i> (Doubleday)	AST:	<i>Campuloclinium megacephalum</i> , <i>Eupatorium</i> sp. indet. 1, <i>Eupatorium</i> sp. indet. 4, <i>Vernonia tomentella</i>
<i>Vanessa</i> Fabricius sp. indet. 1	AST:	<i>Eupatorium</i> sp. indet. 3
<i>Ypthimoides ochracea</i> (Butler)	AST:	<i>Symphypappus compressus</i>
	CLE:	<i>Clethra scabra</i>
Pieridae (whites and yellows)		
<i>Eurema nise tenella</i> (Boisduval)	LYT:	<i>Cuphea glutinosa</i>
	VER:	<i>Verbena hirta</i>
<i>Hesperocharis erota</i> (Lucas)	AST:	<i>Vernonia westiniana</i>

types. Small flowers were predominant. Out of the 65 species with tubular or gullet flowers, for instance, 55.4% had corolla tubes ≤ 5 mm long, whereas only 13.8% had tubes >10 mm long. Nectar was the exclusive or main resource of 71.0% of the species. Although pollinators fed on or collected pollen from more than half of the species, it was the exclusive resource of only 17.7% of the species. Even though we only measured the nectar production of a few species, low nectar production (i.e., less than 2 μ l) prevailed.

The great majority of species presented hermaphroditic flowers (82.3%), and a few were either monoecious (3.2%) or dioecious (8.9%) (Table 2). The latter group only comprised the 11 species of *Baccharis* Mill. (Asteraceae). Seven other species of Asteraceae (5.6%) presented both hermaphroditic and unisexual (ligulate) flowers (gynomonoecism). We detected spontaneous self-pollination in some species including plants that were also pollinated by animals (Table 4).

Table 4. Plant species, time of observation, pollination system, degree of specialization/generalization, and collected and observed pollinators at the Serra da Bocaina grasslands. Abbreviations: N = nocturnal observation; undet. = undetermined pollination system; MONO = monophily, OLIGO = oligophily, POLI = polyphily, HOLO = holophily, n/a = not applicable; BL = large bees, BS = small bees, CO = beetles, DI = flies except syrphids, HB = hummingbirds, LE = butterflies, SSP = spontaneous self-pollination, SY = syrphids, WA = wasps; ? = information to be confirmed; uncoll = uncollected insect pollinators (only observed).

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Amaryllidaceae				
<i>Hippeastrum glaucescens</i>	18.5	hummingbird	MONO	HB - <i>Leucochloris albicollis</i>
Apiaceae				
<i>Eryngium canaliculatum</i>	4	uncertain	n/a	CO - <i>Cardiorhinus</i> sp. indet. 1, Cantharidae sp. indet. 1.
<i>Eryngium horridum</i>	4	several insect groups	HOLO	BS - <i>Plebeia saiqui</i> ; DI - <i>Jurinella</i> cf. <i>corpulenta</i> , Culicidae sp. indet. 1, Curtonotidae sp. indet. 1, Tachinidae sp. indet. 9, Diptera sp. indet. 1; LE - Riordininae sp. indet. 1; SY - uncoll (1 sp.); WA - uncoll (1 sp.)
Apocynaceae				
<i>Gonioanthela hilariana</i>	5.5	wasp/fly	MONO	WA - <i>Polistes cinerascens</i> , <i>Polybia sericea</i>
<i>Mandevilla erecta</i>	18 N	undet.	n/a	not visited
<i>Oxypetalum appendiculatum</i>	7.5	wasp/fly	MONO	WA - <i>Polybia sericea</i>
<i>Oxypetalum sublanatum</i>	11	bee nectar-flower	MONO	BL - <i>Bombus atratus</i>
<i>Tassadia subulata</i>	15	syrphid nectar-flower	MONO	SY - <i>Palpada rufipedes</i> , <i>Toxomerus watsoni</i> , <i>Toxomerus</i> sp. indet. 1, uncoll (1 sp.)
Aquifoliaceae				
<i>Ilex amara</i>	4.5	bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - <i>Augochloropsis</i> cf. <i>cognata</i> , <i>Ceratalictus</i> sp. indet. 1, <i>Plebeia saiqui</i> ; WA - <i>Mischocyttarus drewseni</i> , <i>Polistes billardieri</i> , uncoll Vespidae (1 sp.), Pompilidae (1 sp.)
Asteraceae				
<i>Achyrocline satureioides</i>	6	wasp/fly	POLI	BS - <i>Plebeia droryana</i> ; DI - Tachinidae sp. indet. 8; SY - <i>Toxomerus watsoni</i> , <i>Toxomerus</i> sp. indet. 1, uncoll (2 spp.); WA - <i>Mischocyttarus drewseni</i> , <i>Polistes billardieri</i> , Larrinae sp. indet. 1, Hymenoptera sp. indet. 1, Hymenoptera sp. indet. 7, Hymenoptera sp. indet. 8, Hymenoptera sp. indet. 9, uncoll (1 sp.)
<i>Baccharis aphylla</i>	7	wasp/fly	OLIGO	DI - Sciaridae sp. indet. 1; WA - <i>Mischocyttarus drewseni</i> , Hymenoptera sp. indet. 4, uncoll (1 sp.)
<i>Baccharis curitybensis</i>	4	wasp/fly	MONO	WA - <i>Protonectarina sylveirae</i>

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
<i>Baccharis dracunculifolia</i>	7.5	wasp/fly	OLIGO	<i>Apis mellifera</i> ; DI - <i>Jurinella</i> cf. <i>corpulenta</i> , Tachinidae sp. indet. 8, Diptera sp. indet. 4; WA - <i>Mischocyttarus drewseni</i> , <i>Polistes cinerascens</i> , <i>Pryonyx thomaz</i> , Chrysididae sp. indet. 1, Hymenoptera sp. indet. 14
<i>Baccharis intermixta</i>	4	wasp/fly	MONO	WA - <i>Agelaia vicina</i> , Leucospidae sp. indet. 1, uncoll (1 sp.)
<i>Baccharis leptcephala</i>	4	wasp/fly	OLIGO	SY - <i>Syrphus phaeostigma</i> , <i>Toxomerus watsoni</i> ; WA - uncoll (2 spp.)
<i>Baccharis pentziifolia</i>	9.5	wasp/fly	POLI	<i>Apis mellifera</i> ; CO - Cantharidae sp. indet. 1; DI - uncoll (1 sp.); SY - <i>Toxomerus watsoni</i> , Syrphidae sp. indet. 3; WA - <i>Mischocyttarus drewseni</i> , Hymenoptera sp. indet. 5, Hymenoptera sp. indet. 10, uncoll (1 sp.)
<i>Baccharis platypoda</i>	4	wasp/fly	POLI	<i>Apis mellifera</i> ; BS - uncoll Augochlorini (1 sp.); DI - <i>Jurinella</i> cf. <i>corpulenta</i> , Curtonotidae sp. indet. 1; WA - <i>Polistes cinerascens</i> , <i>Polybia fastidiosuscula</i> , Braconidae sp. indet. 1, Pompilidae sp. indet. 2.
<i>Baccharis tarchonanthoides</i>	4	several insect groups	HOLO	BS - uncoll Augochlorini (1 sp.); CO - Cantharidae sp. indet. 1; DI - Sciaridae sp. indet. 1, uncoll Tachinidae (2 spp.); SY - <i>Toxomerus watsoni</i> , uncoll (1 sp.); WA - <i>Polybia scutellaris</i>
<i>Baccharis</i> sp. indet. 1	4	wasp/fly	MONO	WA - uncoll (1 sp.)
<i>Baccharis</i> sp. indet. 2	7	wasp/fly	POLI	<i>Apis mellifera</i> ; BS - <i>Schwarziana quadripunctata</i> , <i>Trigona spinipes</i> ; DI - Tachinidae sp. indet. 4; WA - <i>Mischocyttarus drewseni</i> , <i>Polistes billardieri</i> , <i>Polybia fastidiosuscula</i> , <i>Protopolybia sedula</i> , Pompilidae sp. indet. 1, Pompilidae sp. indet. 3, Pompilidae sp. indet. 4, Tiphidae sp. indet. 1, uncoll Vespidae (2 spp.)
<i>Baccharis</i> sp. indet. 3	4	wasp/fly	MONO	WA - <i>Brachygastra lecheguana</i> , <i>Polistes billardieri</i>
<i>Barrosoa betoniciiformis</i>	4	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Augochloropsis cyanea</i> ; CO - Cantharidae sp. indet. 1; LE - <i>Sarbia</i> cf. <i>damippe</i> , uncoll (1 sp.)
<i>Campuloclinium megacephalum</i>	11.5	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Melipona quadrifasciata</i> , <i>Augochloropsis cyanea</i> , <i>A. iris</i> , <i>A. cf. cognata</i> , uncoll Augochlorini (1 sp.); BL - <i>Bombus atratus</i> ; CO - Cantharidae sp. indet. 1; DI - <i>Euprepina</i> sp. indet. 1, <i>Paravilla</i> sp. indet. 1, uncoll Bombyliidae (2 sp.); LE - <i>Sarbia</i> cf. <i>damippe</i> , <i>Thespeius</i> sp. indet. 1, <i>Vanessa myrinna</i> , uncoll <i>Vanessa</i> (1 sp.), Hesperidae (1 sp.) uncoll (1 sp.); WA - uncoll Pompilidae (1 sp.), Sphecidae (1 sp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
<i>Chaptalia integerrima</i>	5	several insect groups	HOLO	BS - <i>Paratrigona subnuda</i> , <i>Paroxystoglossa</i> sp. indet. 1, uncoll Halictidae (2 spp.); CO - Cantharidae sp. indet. 1; LE - Pyrrhopyginae sp. indet. 1, uncoll Lycaenidae (1 sp.); WA - <i>Mischocyttarus drewseni</i> , uncoll Eunemidae (1 sp.), Vespidae (1 sp.)
<i>Chaptalia runcinata</i> var. <i>graminifolia</i>	13.5	several insect groups	HOLO	BS - <i>Augochloropsis cyanea</i> , <i>Dialictus</i> sp. indet. 2; DI - <i>Paravilla</i> sp. indet. 1, Diptera sp. indet. 2, Diptera sp. indet. 3, uncoll Bombyliidae (1 sp.); LE - <i>Thecla</i> sp. indet. 1, uncoll Hesperiidae (1 sp.); SY - <i>Toxomerus watsoni</i> , <i>Toxomerus</i> sp. indet. 1, Syrphidae sp. indet. 6
<i>Chromolaena</i> cf. <i>decumbens</i>	7.5	bee nectar-flower	MONO	BL - <i>Bombus atratus</i>
<i>Chromolaena xylorrhiza</i>	4	undet.	n/a	not visited
<i>Eremanthus erythropappus</i>	5	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Melipona bicolor</i> , <i>M. quadrifasciata</i> , <i>Paratrigona subnuda</i> , <i>Schwarziana quadripunctata</i> ; BL - uncoll <i>Bombus</i> (1 sp.); DI - Tachinidae sp. indet. 5; LE - uncoll Hesperiidae (1 sp.), <i>Vanessa</i> (2 spp.); SY - uncoll (1 sp.); WA - uncoll Pompilidae (1 sp.), Sphecidae (1 sp.)
<i>Erigeron maximus</i>	1	several insect groups	HOLO	BS - <i>Coelioxys</i> sp. indet. 1, uncoll Augochlorini (1 sp.); CO - Cantharidae sp. indet. 1; DI -Diptera sp. indet. 6
<i>Eupatorium</i> sp. indet. 1	6	bee nectar-flower	OLIGO	BL - <i>Megachile iheringi</i> , <i>M. terrestris</i> ; LE - <i>Vanessa myrinna</i> , uncoll Lycaenidae (1 sp.)
<i>Eupatorium</i> sp. indet. 2	9.5	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Augochloropsis</i> sp. indet. 1; BL - uncoll <i>Bombus</i> (1 sp.); CO - Cantharidae sp. indet. 1; DI - Tachinidae sp. indet. 1; LE - uncoll Hesperiidae (2 spp.); WA - Hymenoptera sp. indet. 6, uncoll (1 sp.)
<i>Eupatorium</i> sp. indet. 3	1	bee nectar-flower	OLIGO	BS - <i>Melipona bicolor</i> ; LE - <i>Vanessa</i> sp. indet. 1
<i>Eupatorium</i> sp. indet. 1	6	several insect groups	HOLO	BS - <i>Schwarziana quadripunctata</i> , <i>Augochloropsis cyanea</i> ; CO - <i>Astylus sexmaculatus</i> ; DI - uncoll Bombyliidae (1 sp.), Tachinidae (1 sp.); LE - <i>Vanessa myrinna</i> ; SY - uncoll (1 sp.); WA - <i>Mischocyttarus drewseni</i> , <i>Sphex opacus</i>
<i>Gochnatia paniculata</i>	1	wasp/fly	OLIGO	SY - <i>Toxomerus watsoni</i> , uncoll (2 sp.); WA - <i>Mischocyttarus drewseni</i> , <i>Polistes billardieri</i> , uncoll Pompilidae (1 sp.), Vespidae (2 spp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
<i>Grazielia gaudichaudeana</i>	5	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Melipona bicolor</i> , <i>Schwarziana quadripunctata</i> , <i>Augochloropsis cyanea</i> ; CO - Cantharidae sp. indet. 1, uncoll (1 sp.); DI - <i>Cylindromyia dorsalis</i> ; LE - Hesperinae sp. indet. 1; WA - Hymenoptera sp. indet. 13, uncoll (1 sp.)
<i>Hypochaeris gardneri</i>	5.5	bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - <i>Colletes</i> sp. indet. 1; BL - <i>Centris klugi</i>
<i>Lucilia lycopodioides</i>	12.5	wasp/fly	MONO	WA - Hymenoptera sp. indet. 2, uncoll Vespidae (3 spp.)
<i>Mikania lundiana</i>	4.5	bee nectar-flower	POLI	<i>Apis mellifera</i> ; BS - <i>Melipona bicolor</i> , <i>M. quadrifasciata</i> , <i>Paratrigona subnuda</i> , <i>Schwarziana quadripunctata</i> , <i>Pseudagapostemon cyaneus</i> ; LE - uncoll <i>Vanessa</i> (1 sp.); WA - uncoll Pompilidae (1 sp.)
<i>Mikania nummularia</i>	7	wasp/fly	OLIGO	LE - <i>Thecla</i> sp. indet. 1, uncoll Hesperidae (1 sp.); WA - Cercerini sp. indet. 2, Hymenoptera sp. indet. 1, Hymenoptera sp. indet. 2
<i>Mikania sessilifolia</i>	6.5	wasp/fly	POLI	DI - <i>Jurinella</i> cf. <i>corpulenta</i> , Curtonotidae sp. indet. 1, uncoll Curtonotidae (1 sp.), Tachinidae (3 spp.); SY - <i>Toxomerus watsoni</i> , Syrphidae sp. indet. 5; WA - <i>Polistes billardieri</i> , Hymenoptera sp. indet. 3, uncoll Vespidae (2 spp.)
<i>Senecio oleosus</i>	5	syrphid/bee nectar-flower	POLI	BS - <i>Ceratina</i> cf. <i>asuncionis</i> , <i>Pseudagapostemon cyaneus</i> , <i>Coelioxys</i> sp. indet. 1, uncoll Halictini (1 sp.); BL - uncoll <i>Bombus</i> (1 sp.); SY - <i>Toxomerus watsoni</i> , uncoll (2 spp.)
<i>Stevia myriadenia</i>	23	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Paratetrapedia (Lophopedia)</i> cf. <i>pygmaea</i> , <i>P. (Trigonopedia)</i> sp. indet. 1, <i>Augochloropsis</i> sp. indet. 1, <i>Epanthidium autumnale</i> , <i>Coelioxys</i> sp. indet. 2, uncoll Augochlorini (1 sp.); BL - <i>Bombus atratus</i> , <i>B. brasiliensis</i> , uncoll <i>Centris</i> (1 sp.); DI - <i>Paravilla</i> sp. indet. 1, uncoll Bombyliidae (1 sp.); SY - Syrphidae sp. indet. 5, uncoll (1 sp.)
<i>Symphyopappus compressus</i>	5	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Melipona quadrifasciata</i> , <i>Melissoptila aureocincta</i> , <i>Agapostemon</i> sp. indet. 1, <i>Megachile</i> cf. <i>anthidioides</i> ; BL - <i>Bombus atratus</i> , <i>Xylocopa brasilianorum</i> ; DI - Tachinidae sp. indet. 8; LE - <i>Ypthimoides ochracea</i> , uncoll Nymphalidae (2 sp.), Pieridae (1 sp.); WA - Scolidae sp. indet. 1, uncoll (1 sp.)
<i>Vernonia herbacea</i>	8.5	bee nectar-flower	OLIGO	BS - <i>Ceratina</i> cf. <i>asuncionis</i> ; BL - uncoll <i>Bombus</i>

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
<i>Vernonia megapotamica</i>	12	several insect groups	HOLO	BS - <i>Melipona bicolor</i> , uncoll Meliponini (2 spp.), Halictidae (3 spp.); DI - <i>Paravilla</i> sp. indet. 1; LE - <i>Agraulis vanillae</i> ; WA - uncoll Pompilidae (1 sp.), Vespidae (2 spp.)
<i>Vernonia</i> cf. <i>rosea</i>	4	bee nectar-flower	MONO	BL - <i>Centris klugi</i> , uncoll <i>Bombus</i>
<i>Vernonia tomentella</i>	8	bee nectar-flower	POLI	BS - <i>Melipona bicolor</i> , <i>Mesonychium caeruleescens</i> , <i>Ceratina</i> cf. <i>asuncionis</i> , <i>Augochloropsis</i> cf. <i>cognata</i> , <i>A. cyanea</i> , uncoll Halictini (1 sp.); BL - <i>Bombus atratus</i> , <i>Centris klugi</i> , <i>Megachile iheringi</i> , <i>M. terrestris</i> , uncoll <i>Bombus</i> ; LE - <i>Vanessa myrinna</i>
<i>Vernonia tragiaefolia</i>	4	bee nectar-flower	OLIGO	BS - <i>Gaesischia nigra</i> ; BL - uncoll <i>Bombus</i>
<i>Vernonia uestiniana</i>	8	bee nectar-flower	POLI	<i>Apis mellifera</i> ; BS - <i>Melipona bicolor</i> , <i>Plebeia saiqui</i> , <i>Ceratalictus</i> sp. indet. 1, uncoll Meliponini (1 sp.), Halictidae (2 spp.); BL - <i>Bombus atratus</i> , <i>B. brasiliensis</i> , <i>B. morio</i> , uncoll <i>Centris</i> (2 spp.); DI - Tachinidae sp. indet. 6, uncoll Tachinidae (2 spp.); LE - <i>Sarbia</i> cf. <i>xanthippe</i> , Pyrrhopyginae sp. indet. 1, <i>Thecla</i> sp. indet. 1, <i>Hesperocharis erota</i> , uncoll Hesperiididae (1 sp.), Nymphalidae (5 spp.), Pieridae (1 sp.), Sphingidae (1 sp.); WA - Scoliidae sp. indet. 1, uncoll Pompilidae (1 sp.), Vespidae (1 sp.)
Bromeliaceae				
<i>Dyckia tuberosa</i>	10	hummingbird	MONO	HB - <i>Colibri serrirostris</i>
Campanulaceae				
<i>Lobelia camporum</i>	7	bee nectar-flower	OLIGO	BS - <i>Ceratina</i> cf. <i>asuncionis</i> ; BL - <i>Bombus atratus</i> , <i>Centris burgdorfi</i> , uncoll <i>Bombus</i>
<i>Wahlenbergia brasiliensis</i>	15	syrphid/bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - uncoll Augochlorini (2 spp.); SY - <i>Allograpta exotica</i> , <i>Toxomerus watsoni</i> , uncoll (2 spp.)
Clethraceae				
<i>Clethra scabra</i>	7.5	wasp/fly	POLI	<i>Apis mellifera</i> ; BS - <i>Melipona bicolor</i> , <i>Scaptotrigona bipunctata</i> , <i>Schwarziana quadripunctata</i> , <i>Augochloropsis</i> cf. <i>cognata</i> , uncoll Meliponini (2 spp.), Halictidae (3 spp.); CO - Cantharidae sp. indet. 2, <i>Rhinotragus festivus</i> ; DI - Tachinidae sp. indet. 2, Diptera sp. indet. 7, uncoll Sarcophagidae (1 sp.), Tachinidae (1 sp.); LE - <i>Yphthimoides ochracea</i> ; WA - <i>Mischocyttarus drewseni</i> , <i>Synoeca cyanea</i> , <i>Polybia fastidiosuscula</i> , <i>P. minarum</i> , Cercerini sp. indet. 1, Cercerini sp. indet. 2, Hymenoptera sp. indet. 10, uncoll (1 sp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Convolvulaceae				
<i>Convolvulus crenatifolius</i>	4	syrphid/bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - <i>Ceratina</i> sp. indet. 2, uncoll <i>Ceratina</i> (1 sp.); SY - uncoll (1 sp.)
<i>Ipomoea procumbens</i>	6	bee nectar-flower	MONO	BL - <i>Bombus atratus</i> , <i>Xylocopa brasilianorum</i> , uncoll <i>Bombus</i>
<i>Jacquemontia grandiflora</i>	9	bee nectar-flower	POLI	BS - uncoll Meliponini (1 sp.), Tapinotaspidini (1 sp.), Halictidae (3 spp.); BL - <i>Bombus atratus</i> , uncoll <i>Bombus</i> , <i>Centris</i> (1 sp.); WA - uncoll Vespidae (1 sp.)
Cunoniaceae				
<i>Weinmannia organensis</i>	8	several insect groups	HOLO	CO - Cantharidae sp. indet. 2; LE - uncoll (1 sp.); WA - <i>Polybia minarum</i>
Droseraceae				
<i>Drosera montana</i>	6	syrphid/bee pollen-flower	MONO	SY - <i>Toxomerus watsoni</i> , Syrphidae sp. indet. 1, uncoll (1 sp.)
Ericaceae				
<i>Agarista hispidula</i>	38.5	hummingbird, SSP	MONO	HB - <i>Chlorostilbon aureoventris</i> , <i>Leucochloris albicollis</i>
<i>Gaylussacia chamissonis</i>	16.5	bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - <i>Melipona bicolor</i> , <i>Augochloropsis</i> sp. indet. 1, uncoll Meliponini (1 sp.); WA - uncoll <i>Polybia</i> (2 spp.)
<i>Gaylussacia jordanensis</i>	31.5	bee nectar-flower	POLI	<i>Apis mellifera</i> ; BS - <i>Plebeia saiqui</i> , <i>Augochloropsis cyanea</i> , <i>Augochloropsis</i> sp. indet. 1, <i>Ceratalictus</i> sp. indet. 1, <i>Dialictus</i> sp. indet. 1, uncoll Meliponini (1 sp.), Halictidae (1 sp.); BL - <i>Megachile iheringi</i> ; WA - uncoll Vespidae (1 sp.)
Eriocaulaceae				
<i>Paepalanthus paulensis</i>	8	several insect groups	HOLO	BS - <i>Trigona spinipes</i> ; CO - <i>Conognatha</i> sp. indet. 1, <i>Discodon tucumanum</i> ; DI - Sarcophagidae sp. indet. 2, Sciaridae sp. indet. 1, Tachinidae sp. indet. 3, uncoll (1 sp.); LE - uncoll HesperIIDae (1 sp.); SY - <i>Toxomerus watsoni</i> , <i>Toxomerus</i> sp. indet. 1, uncoll (3 spp.); WA - uncoll Vespidae (1 sp.)
<i>Paepalanthus polyanthus</i>	4	several insect groups	HOLO	CO - Cantharidae sp. indet. 1; DI – Diptera sp. indet. 5, Diptera sp. indet. 8, uncoll Bombyliidae (1 sp.); LE - uncoll (1 sp.); SY - <i>Toxomerus watsoni</i> ; WA - <i>Agelaia vicina</i>
Erythroxylaceae				
<i>Erythroxylum microphyllum</i>	6	wasp/fly	OLIGO	BS - <i>Ceratalictus</i> sp. indet. 1, uncoll Meliponini (1 sp.), Augochlorini (2 spp.); WA - <i>Mischocyttarus drewseni</i> , <i>Polistes billardieri</i> , Hymenoptera sp. indet. 2, uncoll Pompilidae (1 sp.), Vespidae (2 spp.)

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Escalloniaceae				
<i>Escallonia farinacea</i>	6	bee nectar-flower	MONO	BS - <i>Colletes</i> sp. indet. 1
Euphorbiaceae				
<i>Croton dichrous</i>	6	wasp/fly	POLI	<i>Apis mellifera</i> ; BS - <i>Augochloropsis</i> cf. <i>cognata</i> , <i>A. cyanea</i> ; DI - uncoll Tachinidae (2 spp.); SY - <i>Toxomerus watsoni</i> ; WA - <i>Mischocyttarus drewseni</i> , <i>Polybia scutellaris</i> , Gasteruptiinae sp. indet. 1, uncoll Vespidae (2 spp.)
Gentianaceae				
<i>Calolisianthus pedunculatus</i>	19.5	undet., SSP	n/a	not visited
<i>Calolisianthus pendulus</i>	38.5	undet., SSP	n/a	not visited
<i>Deianira nervosa</i>	6	syrphid/bee pollen-flower, SSP	MONO	SY - Syrphidae sp. indet. 5
<i>Helia oblongifolia</i>	20 N	undet., SSP	n/a	not visited
<i>Zygostigma australe</i>	8.5	syrphid/bee pollen-flower, SSP	OLIGO	BS - <i>Ceratalictus</i> sp. indet. 1; SY - <i>Allograpta exotica</i> , uncoll (1 sp.)
Gesneriaceae				
<i>Sinningia allagophylla</i>	27	hummingbird	MONO	HB - <i>Clytolaema rubricauda</i> , <i>Colibri serrirostris</i> , <i>Leucochloris albicollis</i> , <i>Stephanoxis lalandi</i>
Hypericaceae				
<i>Hypericum brasiliense</i>	8	syrphid/bee pollen-flower, apomictic	POLI	BS - <i>Schwarziana quadripunctata</i> , Halictini sp. indet. 1; BL - <i>Megachile iheringi</i> ; DI - <i>Cylindromyia dorsalis</i> ; SY - uncoll (1 sp.)
<i>Hypericum ternum</i>	-	uncertain, apomictic	n/a	n/a
Iridaceae				
<i>Alophia geniculata</i>	11	bee pollen-flower	POLI	BS - <i>Melipona bicolor</i> , <i>Plebeia saiqui</i> , <i>Augochloropsis iris</i> , <i>Paroxystoglossa</i> cf. <i>jocasta</i> , <i>Dialictus</i> sp. indet. 1, Halictini sp. indet. 2, uncoll Tapinotaspidini (1 sp.); BL - <i>Bombus atratus</i> ; SY - <i>Toxomerus watsoni</i> , Syrphidae sp. indet. 2
<i>Alophia</i> sp. indet. 1	7	uncertain	n/a	BS - <i>Ceratalictus</i> sp. indet. 1; SY - <i>Allograpta exotica</i>
<i>Calydorea campestris</i>	8.5	syrphid/bee pollen-flower	OLIGO	BS - <i>Plebeia saiqui</i> , <i>Augochloropsis</i> cf. <i>cognata</i> , <i>Dialictus</i> sp. indet. 1; SY - Syrphidae sp. indet. 5, uncoll (2 spp.)
<i>Sisyrinchium micranthum</i>	5	syrphid/bee pollen-flower	OLIGO	BS - <i>Dialictus</i> sp. indet. 1; SY - <i>Allograpta exotica</i>

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
<i>Sisyrinchium vaginatum</i>	21.5	syrphid/bee pollen-flower	OLIGO	<i>Apis mellifera</i> ; BS - uncoll Augochlorini (2 spp.); SY - <i>Toxomerus watsoni</i> , <i>Toxomerus</i> sp. indet. 1, uncoll (1 sp.)
Lamiaceae				
<i>Hyptis lippoides</i>	7	bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - <i>Melipona bicolor</i> , <i>Plebeia saiqui</i> , <i>Trigona spinipes</i> , <i>Augochloropsis</i> cf. <i>cognata</i> , <i>Ceratalictus</i> sp. indet. 1; BL - <i>Bombus atratus</i>
<i>Hyptis plectranthoides</i>	6.5	bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - <i>Ceratalictus</i> sp. indet. 1; BL - <i>Bombus atratus</i> , uncoll <i>Bombus</i>
<i>Hyptis umbrosa</i>	4	bee nectar-flower	OLIGO	<i>Apis mellifera</i> ; BS - <i>Augochloropsis</i> sp. indet. 1, <i>Ceratalictus</i> sp. indet. 1; WA - uncoll Vespidae (2 spp.)
<i>Peltodon radicans</i>	4	bee nectar-flower	MONO	<i>Apis mellifera</i>
Leguminosae				
<i>Chamaecrista</i> sp. indet. 1	6	bee pollen-flower	MONO	BL - <i>Centris klugi</i>
<i>Crotalaria breviflora</i>	7	bee nectar-flower	OLIGO	BS - <i>Anthidium sertanicola</i> ; BL - <i>Bombus atratus</i> , <i>B. brasiliensis</i>
<i>Lupinus velutinus</i>	27	bee pollen-flower, SSP	MONO	BL - <i>Megachile iheringi</i> , <i>M. laeta</i> , <i>Bombus atratus</i> , uncoll <i>Bombus</i> , <i>Megachile</i> (1 spp.)
Lythraceae				
<i>Cuphea glutinosa</i>	24	bee nectar-flower	POLI	<i>Apis mellifera</i> ; BS - <i>Ceratina</i> sp. indet. 1, <i>Mesonychium caeruleescens</i> , <i>Augochloropsis cyanea</i> , <i>Augochloropsis</i> sp. indet. 1, <i>Anthidium sertanicola</i> , <i>Megachile</i> cf. <i>anthidioides</i> ; BL - <i>Bombus atratus</i> , <i>B. brasiliensis</i> , <i>B. morio</i> , <i>Centris klugi</i> ; LE - <i>Eurema nise tenella</i> ; SY - <i>Toxomerus watsoni</i> ; WA - Hymenoptera sp. indet. 3, Hymenoptera sp. indet. 11
Malpighiaceae				
<i>Byrsonima variabilis</i>	16	bee oil-flower	OLIGO	BS - <i>Plebeia saiqui</i> , <i>Augochloropsis</i> cf. <i>cognata</i> , <i>Monoeca</i> sp. indet. 1, <i>Paratetrapedia (Xanthopedia)</i> sp. indet. 1, <i>Centris</i> cf. <i>insularis</i> ; BL - <i>Centris discolor</i> , <i>C. klugi</i> , <i>C. tarsata</i> , <i>Centris (Melacentris)</i> sp. indet. 1, uncoll <i>Centris</i> (2 spp.)
Malvaceae				
<i>Pavonia kleinii</i>	4	bee nectar-flower	MONO	BS - <i>Augochloropsis</i> cf. <i>cognata</i>
<i>Sida</i> sp. indet. 1	6	bee nectar-flower	MONO	BS - <i>Ceratina</i> cf. <i>asuncionis</i> , uncoll <i>Ceratina</i> (1 sp.)
Melastomataceae				
<i>Leandra erostrata</i>	5	uncertain, apomictic?	n/a	not visited

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
<i>Leandra</i> sp. indet. 1	6	uncertain, apomictic?	n/a	not visited
<i>Leandra</i> sp. indet. 2	11	uncertain, apomictic?	n/a	not visited
<i>Leandra</i> sp. indet. 3	6.5	uncertain, apomictic?	n/a	not visited
<i>Microlicia isophylla</i>	14.5	uncertain, apomictic?	n/a	not visited
<i>Tibouchina frigidula</i>	24	bee pollen-flower	MONO	BL - <i>Bombus atratus</i> , <i>Xylocopa brasilianorum</i> , <i>Centris discolor</i> , uncoll <i>Bombus</i> , <i>Centris</i> (2 spp.)
<i>Tibouchina martialis</i>	4	bee pollen-flower	MONO	BL - <i>Xylocopa brasilianorum</i> , uncoll <i>Centris</i> (1 sp.)
<i>Tibouchina minor</i>	10	bee pollen-flower	OLIGO	BS - uncoll Augochlorini (1 sp.); BL - <i>Bombus atratus</i> , <i>Centris klugi</i> , uncoll <i>Centris</i> (2 spp.)
<i>Trembleya parviflora</i>	6	bee pollen-flower	MONO	BS - <i>Melipona bicolor</i>
<i>Trembleya phlogiformis</i>	7	bee pollen-flower	OLIGO	BS - <i>Augochloropsis</i> sp. indet. 1; BL - <i>Bombus atratus</i>
Ochnaceae				
<i>Ouratea semiserrata</i>	7	bee pollen-flower	OLIGO	BS - <i>Melipona bicolor</i> , <i>Dialictus</i> sp. indet. 1; BL - uncoll <i>Centris</i> (1 sp.)
Orchidaceae				
<i>Epidendrum secundum</i>	14	undet.	n/a	not visited
<i>Habenaria parviflora</i>	5, 13 N	undet.	n/a	not visited
<i>Oncidium barbaceniae</i>	19.5	uncertain	n/a	uncoll <i>Bombus</i>
<i>Oncidium blanchetii</i>	14	undet.	n/a	not visited
<i>Oncidium</i> sp. indet. 1	14	undet.	n/a	not visited
Orobanchaceae				
<i>Esterhazyia macrodonta</i>	72.5	hummingbird	MONO	HB - <i>Leucochloris albicollis</i>
Polygalaceae				
<i>Polygala brasiliensis</i>	6.5	bee nectar-flower, SSP?	MONO	BS - uncoll Augochlorini (1 sp.)
<i>Polygala cneorum</i>	10	bee nectar-flower, SSP?	MONO	BS - <i>Augochloropsis</i> sp. indet. 1

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Rubiaceae				
<i>Borreria capitata</i>	8.5	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Augochloropsis</i> cf. <i>cognata</i> , <i>Ceratalictus</i> sp. indet. 1; DI - <i>Exoprosopa</i> sp. indet. 1, uncoll Sarcophagidae (1 sp.); SY - <i>Pseudodoros clavatus</i> , <i>Toxomerus watsoni</i> , <i>Toxomerus</i> sp. indet. 1, uncoll (1 sp.); WA - Hymenoptera sp. indet. 2, uncoll Vespidae (1 sp.)
<i>Borreria tenella</i>	5	wasp/fly	OLIGO	BS - <i>Ceratalictus</i> sp. indet. 1; WA - <i>Polybia sericea</i> , Hymenoptera sp. indet. 2, uncoll Vespidae (2 spp.)
<i>Declieuxia cordigera</i> var. <i>angustifolia</i>	7	bee nectar-flower	POLI	BS - Augochlorini sp. indet. 1, uncoll Augochlorini (1 sp.); BL - <i>Bombus atratus</i> , <i>Centris burgdorfi</i> , uncoll <i>Bombus</i> ; LE - uncoll Hesperidae (1 sp.); WA - uncoll Vespidae (1 sp.)
<i>Galianthe angustifolia</i>	24	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Mesonychium caerulescens</i> , <i>Augochloropsis cyanea</i> , uncoll Augochlorini (2 spp.); BL - <i>Bombus atratus</i> , <i>B. morio</i> , uncoll <i>Centris</i> (2 spp.); DI - Curtonotidae sp. indet. 2, Sarcophagidae sp. indet. 1, Tachinidae sp. indet. 7; LE - uncoll Hesperidae (1 sp.); SY - <i>Allograpta exotica</i> , uncoll (2 spp.); WA - <i>Bicyrtes paranae</i> , <i>Sphex dorsalis</i> , <i>Polybia fastidiosuscula</i> , Hymenoptera sp. indet. 15, uncoll Vespidae (2 spp.)
<i>Galianthe brasiliensis</i>	8	several insect groups	HOLO	<i>Apis mellifera</i> ; BS - <i>Augochloropsis</i> cf. <i>cognata</i> , <i>Augochloropsis cyanea</i> , <i>Augochloropsis</i> sp. indet. 1, <i>Ceratalictus</i> sp. indet. 1; DI - Tachinidae sp. indet. 1, Tachinidae sp. indet. 4; LE - <i>Thecla</i> sp. indet. 1; SY - <i>Pseudodoros clavatus</i> , <i>Toxomerus watsoni</i> , uncoll (1 sp.); WA - <i>Mischocyttarus drewseni</i> , <i>Polistes billardieri</i> , Tenthredinidae sp. indet. 1, Hymenoptera sp. indet. 12, uncoll Pompilidae (1 sp.), Sphecidae (1 sp.), Vespidae (3 spp.)
<i>Galium hypocarpium</i>	11.5	wasp/fly	OLIGO	DI - <i>Trupanea</i> sp. indet. 1, WA - Eurytomidae sp. indet. 1
Solanaceae				
<i>Solanum aculeatissimum</i>	9.5	bee pollen-flower	MONO	BS - <i>Augochloropsis cyanea</i>
<i>Solanum americanum</i>	8.5	bee pollen-flower	MONO	BS - uncoll Augochlorini (1 sp.)
<i>Solanum pseudocapsicum</i>	5.5	bee pollen-flower	MONO	BS - <i>Augochloropsis cyanea</i> , <i>Augochloropsis</i> sp. indet. 1
<i>Solanum swartzianum</i>	4.5	bee pollen-flower	MONO	BS - <i>Augochloropsis cyanea</i>
<i>Solanum viarum</i>	13	bee pollen-flower	MONO	BS - <i>Augochloropsis cyanea</i>

Table 4. Continued.

Family/Species	Time of observ. (hours)	Pollination system	Degree of specialization/ generalization	Pollinator species
Verbenaceae				
<i>Verbena hirta</i>	10	bee nectar-flower	POLI	<i>Apis mellifera</i> ; BS - <i>Mesonychium caerulescens</i> , <i>Ceratina</i> cf. <i>asuncionis</i> , <i>Pseudaugochlora</i> cf. <i>graminea</i> , Halictini sp. indet. 2; BL - <i>Bombus atratus</i> , <i>B. brasiliensis</i> , <i>B. morio</i> , <i>Xylocopa brasilianorum</i> , <i>Centris tarsata</i> , <i>Megachile laeta</i> ; LE - <i>Urbanus</i> sp. indet. 1, <i>Eurema nise</i> , uncoll <i>Vanessa</i> (1 sp.); SY - uncoll (2 spp.); WA - uncoll Vespidae (1 sp.)
Violaceae				
<i>Viola cerasifolia</i>	27	bee pollen-flower	MONO	BS - <i>Anthrenoides</i> sp. indet. 1, <i>Augochlorodes turrifaciens</i> , <i>Dialictus</i> sp. indet. 1
Xyridaceae				
<i>Xyris asperula</i>	4	syrphid/bee pollen-flower	OLIGO	BS - <i>Augochloropsis cyanea</i> , uncoll Meliponini (1 sp.), Augochlorini (1 sp.); SY - <i>Toxomerus watsoni</i> , Syrphidae sp. indet. 1, uncoll (2 spp.)
<i>Xyris tortulla</i>	6	syrphid/bee pollen-flower	OLIGO	BS - <i>Paratetrapedia</i> cf. <i>pygmaea</i> ; SY - <i>Toxomerus watsoni</i> , Syrphidae sp. indet. 4, uncoll (2 spp.)

Table 5. Number of plant species exclusively, mainly, and secondarily pollinated by each pollinator group at the Serra da Bocaina grasslands. Percentages are given in parentheses (n = 106 plant species). Because many species are pollinated by two to six pollinator groups the sum of the totals exceeds 100%.

Pollinator group	Role in pollination			
	Exclusive	Main*	Secondary or indistinct	Total
Small bees §	12 (11.3%)	21 (19.8%)	38 (35.9%)	71 (67.0%)
Wasps	7 (6.6%)	15 (14.2%)	26 (24.5%)	48 (45.3%)
Large bees §	8 (7.6%)	18 (17.0%)	10 (9.4%)	36 (34.0%)
Syrphids	3 (2.8%)	12 (11.3%)	18 (17.0%)	33 (31.1%)
Other flies	0	3 (2.8%)	26 (24.5%)	29 (27.3%)
Butterflies	0	2 (1.9%)	23 (21.7%)	25 (23.6%)
Beetles	0	0	13 (12.3%)	13 (12.3%)
Hummingbirds	5 (4.7%)	0	0	5 (4.7%)

* Includes plant species that have multiple pollinator groups but only one or two are the main pollinator group(s) (see methods section of text).

§ *Apis mellifera* not included.

B. POLLINATOR AGENTS

A wide array of pollinator agents were recorded (Tables 3, 4). Hymenopterans, followed by dipterans, were the most important pollinators, and all insect groups except large bees were found more often as secondary agents than as exclusive or main pollination agents (Table 5). Hummingbirds, which were the only vertebrate group, acted as exclusive pollinators (Table 5).

Hymenoptera. Bees and/or wasps were among the pollinator agents of 98 of the 101 plant species pollinated by insects. In addition, hymenopterans were the pollinators of three-fourths of the plants pollinated by one group only (Table 5). We recorded at least 54 native species of bees (Table 3). The families Apidae (including “Anthophoridae”), Halictidae, and Megachilidae were represented by 28, 16, and 8 species, respectively. Andrenidae and Colletidae were only represented by one species each. Halictidae bees—owing mainly to Augochlorini species—pollinate about half of the species in this community. Meliponini bees played a minor role in pollination, occasionally pollinating some generalist plant species, and acted more as pollen thieves in several species (e.g., *Baccharis* and Melastomataceae species, Fig. 1I). However, *Melipona bicolor*—which is markedly larger than other Meliponini bees in that area—was an important pollinator of several species (Fig. 1B, Table 3). Small and large bees belonging to Megachilidae pollinated 12 species from six families. The large Apidae bees belonging to the genera *Bombus*, *Xylocopa* Latr., and *Centris* Fabr. also were important pollinators in the community. The three bumblebee species—mainly *Bombus atratus*—pollinated at least 29 species, and they were either the most frequent or the exclusive pollinators of 12 of

them. We recorded at least 46 species of wasps acting as pollinators, the most important of which were the social Vespidae, in particular *Polistes* Latr. species, followed by Pompilidae and Sphecidae.

The introduced honeybee, *Apis mellifera*, acted as a pollen robber in *Sinningia allagophylla* but pollinated the other 31 species they visited (Table 3). These bees were frequent visitors to some species classified as having bee nectar-flower pollination systems (i.e., pollinated by bees in search of nectar; see “Pollination Systems” below), such as *Ilex amara*, *Gaylussacia chamissonis*, *G. jordanensis*, and *Cuphea glutinosa*. Honeybees were the most important pollinators of the three *Hyptis* Jacq. species (Lamiaceae) and the only flower visitor for the other Lamiaceae, *Peltodon radicans*.

Diptera. Syrphids constituted a noticeable group of pollinators in the community, feeding on both nectar- and pollen-flowers. Species of the genus *Toxomerus* Macq. were particularly important and, for instance, *T. watsoni* acted as a pollinator of 21 species (Table 3). Flies other than syrphids were represented mainly by Tachinidae and Bombyliidae (beeflies) and, usually, were secondary or indistinct pollinators of polyphilous or holophilous species (Fig. 2B, Tables 5, 6).

Lepidoptera. Pollination by lepidopterans (Fig. 2I) was poorly represented. Butterflies (“Rhopalocera”) and diurnal moths (“Heterocera”) generally played a secondary role for plants pollinated mainly by bees (Tables 4, 5, 6). They were among the most frequent pollinators of only a few Asteraceae species. Butterflies belonging to the genus *Vanessa* Fabr. (Nymphalinae) were the most frequent flower visitors of this group. In spite of the scarcity of their visits to flowers, many butterflies were recorded during the summer and fall, and small butterflies belonging to Hesper-

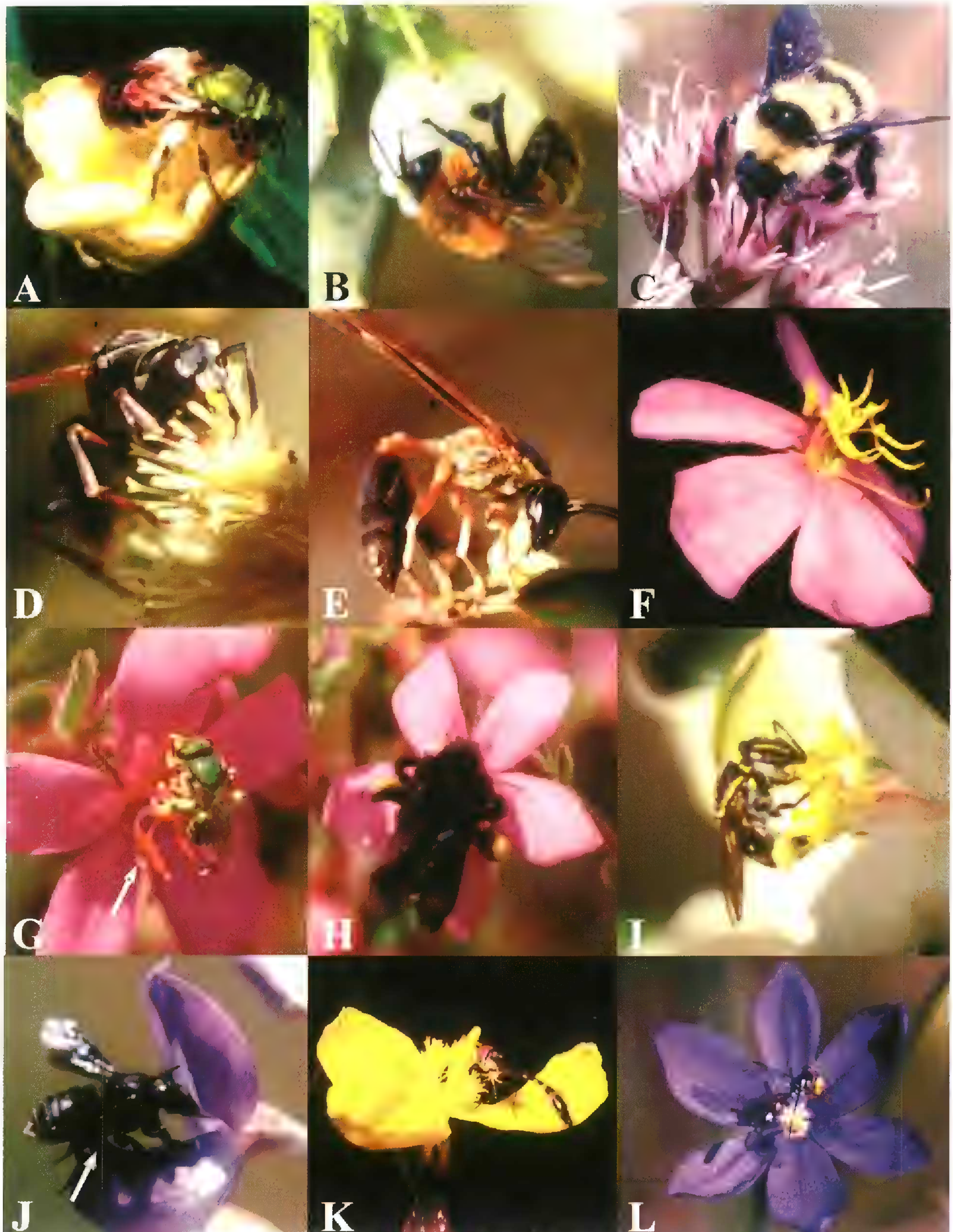


Figure 1. Flowers and pollinators at the Serra da Bocaina grasslands. A–C. Bee nectar-flowers. —A. *Augochloropsis* aff. *cognata* (Halictidae) visiting a flower of *Paronia kleinii* (Malvaceae). —B. A stingless bee *Melipona bicolor* (Apidae) entering a bell-shaped flower of *Gaylussacia chamissonis* (Ericaceae). —C. *Bombus brasiliensis* (Apidae) visiting a head of *Vernonia westiniana* (Asteraceae). D, E. Wasp/fly flowers. —D. *Polistes billardieri* (Vespidae) visiting a head of *Gochnatia paniculata* (Asteraceae), which is also pollinated by syrphids. —E. *Polybia sericea* (Vespidae) visiting a flower of *Gonioanthela hilariana* (Apocynaceae). F–J. Bee pollen-flowers. —F. A flower of *Tibouchina minor* (Melastomataceae). Note the long poricidal anthers. —G. *Augochloropsis* sp. indet. 1 collecting pollen by vibration from a single anther of a *Trembleya phlogiformis* (Melastomataceae) flower. This bee only occasionally touches the stigma (arrow). —H. *Bombus atratus* collecting pollen by vibration in *Trembleya phlogiformis*, which is mainly pollinated by this bee. —I. *Paratrigona subnuda* (Apidae) collecting pollen from a flower of *Trembleya parviflora*. This bee removes pollen from the anther by inserting its proboscis and acts as pollen thief since it does not transfer pollen to the stigma of this species, which is pollinated by another stingless bee, *Melipona bicolor*. —J. *Megachile iheringi* (Megachilidae) collecting pollen from a keel shaped flower of *Lupinus velutinus* (Leguminosae). Note the bee abdomen touching the keel petals (arrow). K, L. Syrphid/small bee pollen-flowers. —K and L. Syrphids species feeding directly on pollen from flowers of *Ayris tortulla* (Xyridaceae) and *Calydorea campestris* (Iridaceae), respectively. See Table 2 for flower measurements.



Figure 2. Flowers and pollinators in the Serra da Bocaina grasslands. Flowers pollinated by several insect groups: —A–C. Species of three pollinator groups visiting the heads of *Eupatorium* sp. indet. 1 (Asteraceae), respectively, a wasp (*Sphex opacus*, Sphecidae), a bee fly (Bombyliidae), and a small bee (*Augochloropsis cyanea*, Halictidae). Oil-flower: —D. *Paratetrapedia* sp. indet. 1 collecting pollen from flowers of *Byrsonima variabilis* (Malpighiaceae). Note the flower oil-glands or elaiophores (arrow). —E. *Centris* cf. *insularis* (Apidae) collecting oil from flowers of *Byrsonima variabilis* (Malpighiaceae). Syrphid/small bee nectar-flowers: —F. *Ceratina* sp. indet. 2 (Apidae) visiting a flower of *Convolvulus crematifolius* (Convolvulaceae). —G. *Pseudagapostemon cyaneus* (Halictidae) visiting a head of *Senecio oleosus* (Asteraceae). Minor pollinator groups: —H. A beetle (Cantharidae sp. indet. 2) visiting a flower of the mainly wasp-pollinated *Clethra scabra* (Clethraceae). —I. A butterfly, *Thecla* sp. indet. 1 (Lycenidae), visiting the generalist flowers of *Galianthe brasiliensis* (Rubiaceae). Doubtful pollination systems: —J. A female *Monocera* sp. indet. 1 (Apidae) with a pollinarium of a species of *Oncidium* (Orchidaceae) attached to its clypeus. This digger bee was captured while collecting oil on flowers of *Byrsonima variabilis*, and its role in the pollination of *Oncidium* species is uncertain. —K. Flower of *Helia oblongifolia* (Gentianaceae). Floral traits point to pollination by nocturnal moths, but no pollinators were observed. —L. Flower of *Calolisianthus pedunculatus* (Gentianaceae). The attractive flowers of this species seem to be adapted to pollination by hummingbirds, but they are nectarless and spontaneously self-pollinated. See Table 2 for flower measurements.

Table 6. The number (and percentage) of plant species that are monophilous (most specialized), oligophilous, polyphilous, and holophilous (most generalized) within each pollination system and pollinator group at the Serra da Bocaina grasslands.

	Monophily	Oligophily	Polyphily	Holophily	Total of species†
All species	36 (34.0%)	32 (30.2%)	18 (17.0%)	20 (18.8%)	106
Pollination system					
Small and large bee nectar-flowers*	10 (33.3%)	12 (40.0%)	8 (26.7%)	0	30
Wasp and wasp/fly nectar-flowers	7 (36.4%)	8 (31.8%)	7 (31.8%)	0	22
Several insect groups	0	0	0	20 (100%)	20
Small and large bee pollen-flowers	11 (73.3%)	3 (20.0%)	1 (6.7%)	0	15
Syrphid and syrphid/small bee pollen-flowers	2 (22.2%)	6 (66.7%)	1 (11.1%)	0	9
Hummingbird flowers	5 (100%)	0	0	0	5
Syrphid/bee nectar-flowers	0	2 (66.7%)	1 (33.3%)	0	3
Small and large bee oil-flowers	0	1 (100%)	0	0	1
Syrphid nectar-flowers	1 (100%)	0	0	0	1
Undetermined or uncertain	—	—	—	—	18
Pollinator groups‡					
Small bees ‡	12 (16.9%)	25 (35.2%)	16 (22.5%)	18 (25.4%)	71
Wasps	7 (14.6%)	11 (22.9%)	14 (29.2%)	16 (33.3%)	48
Large bees ‡	8 (22.2%)	12 (33.3%)	10 (27.8%)	6 (16.7%)	36
Syrphids	3 (9.1%)	10 (30.3%)	9 (27.3%)	11 (33.3%)	33
Other flies	0	3 (10.3%)	9 (31.1%)	17 (58.6%)	29
Butterflies	0	3 (12.0%)	6 (24.0%)	16 (64.0%)	25
Beetles	0	0	2 (15.4%)	11 (84.6%)	13
Hummingbirds	5 (100%)	0	0	0	5

† Does not include species where the pollination system was not determined or was uncertain.
* Includes *Gaylussacia chamissonis* and the four species of Lamiaceae pollinated exclusively or mainly by *Apis mellifera*.
§ Since many species are pollinated by more than one pollinator group, the sum total of plant species exceeds 106.
‡ *Apis mellifera* not included.

iinae (probably species of *Corticea* Evans) were very common in all seasons at the study sites.

Coleoptera. Beetles pollinated a few species and always acted as secondary or indistinct pollinators (Tables 5, 6). Cantharidae (Fig. 2H), most particularly Cantharidae sp. indet. 1, which pollinated 10 species (Table 3), was the only beetle family with a notable importance in pollination at the community level.

Vertebrata. The interactions between hummingbird-pollinated plants and their agents were the most specialized at the community level. We recorded five Trochilinae species in the study areas (Fig. 3, Table 3). These species could be observed year-round in the high-altitude forest and grasslands, except

Colibri serrirostris, which seems to migrate to the highlands during the wet season.

POLLINATION SYSTEMS

The nine pollination systems differed markedly with regard to their number of species. For instance, the three most important systems, respectively, small and large bee nectar-flowers, wasp and wasp/fly nectar-flowers, and several insect groups, encompass 72 species (68% of the 106 species total; Table 6). On the other hand, two of the systems, respectively small and large bee oil-flowers and syrphid nectar-flowers, only comprise one species each (Tables 4, 6).

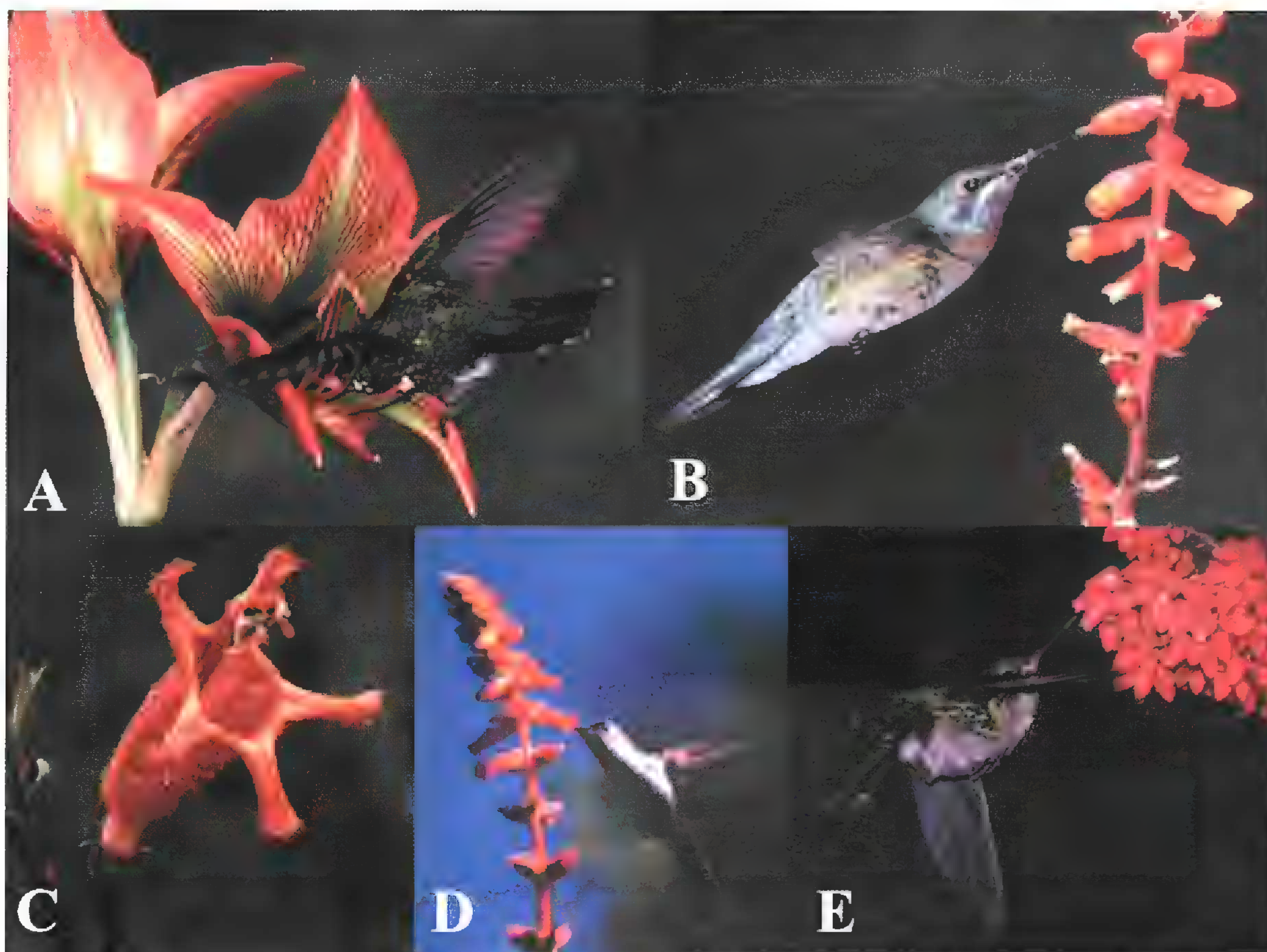


Figure 3. Hummingbirds and their flowers in the Serra da Bocaina grasslands. —A. *Leucochloris albicollis* visiting a very large flower of *Hippeastrum glaucescens* (Amaryllidaceae). Note the hummingbird's foot gripping the inferior tepal. —B. A female *Colibri serrirostris* visiting flowers of *Dyckia tuberosa* (Bromeliaceae). Note pollen on the bird's bill and forehead. —C. Flower of *Esterhazyia macrodonta* (Orobanchaceae), which is pollinated by *L. albicollis*. —D. A female *Stephanoxis lalandi* visiting flowers of *Sinningia allagophylla* (Gesneriaceae). —E. A female *Chlorostilbon aureoventris* visiting flowers of *Agarista hispidula* (Ericaceae); originally published by Plant Systematics and Evolution, 2006, Springer-Verlag; reproduced with permission. See Table 2 for flower measurements.

A. NECTAR-FLOWERS POLLINATED MAINLY BY SMALL AND LARGE BEES

Plants of this group had flowers pollinated mainly by large or small bees that were searching for nectar (Fig. 1A–C). This group shows great variability in floral traits, and we observed specific associations with pollinators among its species. As a whole, this group is the most representative pollination system of the community (Table 6).

This plant group first includes five species pollinated exclusively by small bees. Species of Malvaceae (Fig. 1A) and Polygalaceae were pollinated by Ceratinini or Halictidae bees, and *Escallonia farinacea* was pollinated only by *Colletes* sp. indet. 1 (Colletidae) (Table 4). An important sub-group comprises species predominantly pollinated by small bees, in which wasps either were rare—*Mikania lundiana*, *Hyptis umbrosa*, and *Gaylussacia jordanensis*—or acted as secondary agents—*Ilex amara* and *Gaylussacia chamissonis* (Fig. 1B). The last three species have white, bell-shaped flowers.

Large bees were the exclusive pollinators of the large flowers of *Ipomoea procumbens* and *Oxypetalum sublanatum*, and also, of two Asteraceae

species, *Chromolaena* cf. *decumbens* and *Vernonia* cf. *rosea*. Likewise, *Lobelia camporum* and *Hyptis lippoides* were mainly pollinated by large bees, although small bees acted as their secondary pollinators. Despite their typically melittophilous flowers (sensu Faegri & van der Pijl, 1979), *Cuphea glutinosa* and *Verbena hirta* were each pollinated by five different agents, of which large bees were by far the most frequent ones; for *C. glutinosa*, the pollen load deposited on the stigmas in a single large bee visit was significantly higher than that deposited by small bees, wasps, or syrphids (L. Freitas, unpubl. data). Both *C. glutinosa* and *V. hirta* bloom continuously (Table 1) and are among the most common plants in the study area.

Plant species pollinated by large bees produced larger quantities of nectar than the other insect-pollinated species, which typically secreted less than 2 μ l of nectar per flower per day. *Oxypetalum sublanatum* and *Lobelia camporum* flowers, for instance, secreted 5.5–8 μ l ($n = 10$) and 4–7 μ l ($n = 17$) of nectar per day, respectively.

Another sub-group in this system is composed of species in which both large and small bees seemed to be the main pollinators—*Hypochaeris*

gardneri, *Vernonia herbacea*, *V. tragiaefolia*, *Jacquemontia grandiflora*, *Hyptis plectranthoides*, *Crotalaria breviflora*, and *Declieuxia cordigera*. The pollination systems of some species of Asteraceae diverge slightly from this last sub-group, because, in addition to small or large bees as their main pollinators, butterflies were either important agents—*Eupatorium* sp. indet. 3 and *Vernonia westiniana* (Fig. 1C)—or secondary agents—*Eupatorium* sp. indet. 1 and *V. tomentella*.

B. NECTAR-FLOWERS POLLINATED EITHER BY WASPS OR BY WASPS AND DIPTERA

This group includes species from several families, such as *Gonioanthela hilariana* (Fig. 1E), *Oxypetalum appendiculatum*, *Erythroxylum microphyllum*, *Croton dichrous*, *Clethra scabra* (Fig. 2H), and *Borreria tenella*, for which wasps were either the exclusive pollinator or the main pollinator, usually associated with flies. Wasps were also either the main or the exclusive pollinators of many Asteraceae, e.g., *Achyrocline satureioides*, *Gochnatia paniculata* (Fig. 1D), *Lucilia lycopodioides*, and *Mikania nummularia*, and of all species of the genus *Baccharis* except *B. tarchonanthoides* and *B. dracunculifolia*. In the latter, as well as in *Mikania sessilifolia* and the spontaneously self-pollinated *Galium hypocarpium*, pollination by flies and wasps was equally important.

Flowers of this group typically have easily accessible nectar and are usually greenish. Predominant flower shapes are short tube (e.g., *Mikania* Willd.) and dish (e.g., *Gonioanthela* Malme and *Erythroxylum* P. Browne), but flowers may be large in width, allowing the insect to enter and reach the nectar (e.g., *Oxypetalum appendiculatum*). Wasps carry few pollen grains on their bodies, and some species belonging to this pollination system may be additionally pollinated by wind.

C. POLLEN-FLOWERS POLLINATED BY SMALL AND LARGE BEES

Nectarless flowers with poricidal anthers are the most characteristic of this system, which includes species of Melastomataceae and Solanaceae, among others (Fig. 1F–I). Plants of this group were pollinated by large and small bees, which collected pollen by vibration. Large Apidae bees—belonging to the genera *Bombus*, *Xylocopa*, and *Centris*—were the exclusive pollinators of *Tibouchina frigidula*, *T. martialis*, and *Chamaecrista* sp. indet. 1. Large bees were also the pollinators of *Tibouchina minor* (Fig. 1F), *Trembleya phlogiformis* (Fig. 1G–H), and *Ouratea semiserrata*, in addition to such small bees as *Melipona bicolor* and

some Halictidae species. The remaining plant species with poricidal anthers—*Trembleya parviflora* (Fig. 1H) and the five *Solanum* L. species—have relatively small flowers, which were only pollinated by small bees. Four species of *Solanum* were exclusively pollinated by the same small bee—*Augochloropsis cyanea* (Halictidae). This bee (Fig. 2C) is endemic to the Brazilian coastal range and is markedly larger (mean body length 10.1 ± 0.99 mm, $n = 10$) than other Halictidae species in the study area.

Bees searching for pollen also pollinated some flowers without poricidal anthers. *Viola cerasifolia* flowers have five anthers opening longitudinally, but their androecium is arranged so as to function as a single poricidal anther. This species was mainly pollinated by small *Anthrenoides* Ducke bees (Andrenidae), which showed a singular pollen collecting behavior on these flowers, in addition to vibration (see Freitas & Sazima, 2003a for details).

The nectarless flag-shaped flowers of *Lupinus velutinus* were only pollinated by large bees belonging to the genera *Bombus* and *Megachile* Latr. (Fig. 1J). During the bumblebee visits, the weight of the bee flexed the wing petals downward and pollen was therefore pressed out in portions, at the tip of the keel (“macaroni pump” type of pollen presentation, sensu Endress, 1994), which contacted the abdomen of the bee. However, pollen collection by bumblebees was usually improved by vibration. Leafcutter bees seem to lack the necessary weight to flex the wings and press pollen out of the keel. During their visits to a flower, these bees used their head as a lever, and the wings were thus depressed by their front and middle legs (Fig. 1J). The hind legs stroked the sides of the keel, forcing a stream of pollen out of the keel beak, and pollen was then packed on the ventral abdomen of the bee (“milking action,” sensu Wainwright, 1978).

Bombus atratus, collecting pollen by vibration, was the effective pollinator of *Alophia geniculata* flowers, although its visits were infrequent. Small bees and syrphids frequently fed on pollen of this species, but they only occasionally pollinated its large flowers. A similar pollination system is expected for *Alophia* sp. indet. 1, although we were unable to record any large bees on its flowers (Table 4).

D. POLLEN-FLOWERS POLLINATED EITHER BY SYRPHIDS OR BY SMALL BEES AND SYRPHIDS

Syrphids were the exclusive pollinators of *Drosera montana* and *Deianira nervosa* and the co-pollinators, in association with small bees, of *Zygostigma australe*, *Calydorea campestris*, *Sisyrinchium vaginatum*, *Xyris asperula*, and *Xyris tortulla* (Fig. 1K–L). Species in this group typically bear small, dish-shaped, actino-

morphic, and vividly colored pollen-flowers. Pollen grains are easily accessible to pollinators of these species because their anthers open longitudinally. Flowers of *Sisyrinchium micranthum* bear oil-secreting trichomes at the base of the staminal column (see Cocucci & Vogel, 2001, Truyló et al., 2002). However, we failed to detect any oil-collecting bees on these flowers, which were pollinated by syrphids and small pollen-collecting bees.

E. NECTAR-FLOWERS POLLINATED BY SEVERAL INSECT GROUPS (SIG)

This group contains species pollinated by three or more functional groups with similar importance (holophily). The SIG system includes some species with very small, greenish flowers—*Eryngium horridum* (and probably *E. canaliculatum*), *Paepalanthus paulensis*, *P. polyanthus*, and *Weinmannia organensis*—that fit the “diverse small insects” (d.s.i.) syndrome of Bawa et al. (1985).

The SIG system also includes species from several Asteraceae genera (*Baccharis tarchonanthoides*, *Barrosoa betonicifformis*, *Campuloclinium megacephalum*, *Chaptalia integerrima*, *C. runcinata*, *Eremanthus erythropappus*, *Erigeron maximus*, *Eupatorium* sp. indet. 2, *Eupatorium* sp. indet. 4 [Fig. 2A–C], *Grazielia gaudi-chau-deana*, *Stevia myriadenia*, *Symphyopappus compressus*, and *Vernonia megapotamica*) and three Rubiaceae species (*Borreria capitata*, *Galianthe angustifolia*, and *G. brasiliensis* [Fig. 2I]). Large insects, such as bumblebees and Pompilidae wasps, were among the pollination agents of some holophilous species of Asteraceae and Rubiaceae, which thus differed from the species of Apiaceae, Eriocaulaceae, and Cunoniaceae, which have very small flowers (Table 4).

F. HUMMINGBIRD POLLINATED FLOWERS

Hummingbirds were the exclusive pollinators of five species from five families. These species bear tubular/urceolate flowers that make them easily distinguishable from flowers of other species in this community (Fig. 3). Except the nectarless, spontaneously self-pollinated flowers of *Calolisianthus pedunculatus* (Fig. 2L), all species with red-orange flowers were pollinated by hummingbirds.

Each of these plant species was pollinated by one to four hummingbird species (Tables 3, 4). *Leucochloris albicollis* was the main visitor in the study area, pollinating four species and acting as the single pollinator of *Esterhazyia macrodonta* and *Hippeastrum glaucescens*. This *Hippeastrum* Herb. species bears very large flowers (tepals ca. 140 cm long), and the birds needed to perch on one of the inferior tepals to

reach the nectar at the flower base (Fig. 3A). Pollen was deposited mainly on their wings. On the other hand, *Esterhazyia macrodonta* has protandrous flowers (Fig. 3C) that last up to six days. Nectar removal in the first days of anthesis strongly affects nectar production (see Freitas & Sazima, 2001 for details).

Sinningia allagophylla bears a long hairy inflorescence with more than 40 flowers, which last up to seven days and present partial herkogamy associated with protandry. This gesneriad was mainly pollinated by *Leucochloris albicollis* and *Stephanoxis lalandi* (Fig. 3D), but also by *Colibri serrirostris* and *Clytolaema rubricauda*. The flower disposition along the inflorescence of *Dyckia tuberosa* resembles that of *S. allagophylla* (Fig. 3B, D), and we only observed *Colibri serrirostris* females pollinating this terrestrial bromeliad (Fig. 3B). *Agarista hispidula* bears dozens of flowers arranged in dense inflorescences (Fig. 3E). Flowers are urceolate with poricidal anthers, and pollen is secondarily presented on hairs at the corolla opening. It was pollinated very early in the morning, mainly by the small *Chlorostilbon aureoventris* (Fig. 3E), but also by *Leucochloris albicollis* (see Freitas et al., 2006 for details). In general, ornithophilous species were rare in these grasslands. We found only four, seven, and eight flowering individuals of, respectively, *Agarista hispidula*, *Dyckia tuberosa*, and *Hippeastrum glaucescens* in the study areas. It was common for there to be < 10 *Esterhazyia macrodonta* plants along each 1 km transect; however, along one exceptional transect we found 55 flowering individuals, whose nectar features were also studied (Freitas & Sazima, 2001). In contrast, *S. allagophylla* was common in many places in the Serra da Bocaina. Individuals of this species were usually distributed in small clusters (three to eight plants) separated from each other by many meters. However, *S. allagophylla* plants occurred in large clusters in some areas—with dozens of individuals per 100 m²—probably due to clonal reproduction. *Esterhazyia* Mikan., *Agarista* D. Don, and *Dyckia* Schult. f. plants were rarely visited, receiving, respectively, 0.05, 0.18, and 0.20 visits per hour (see Table 4 for times of observation). Each plant of *Hippeastrum glaucescens* received ca. one visit every two hours. Although plants of *Sinningia* Nees growing in small clusters received ca. only one visit every three hours, when in large clusters, hummingbirds visited each patch between three and six times per hour so that most individuals were visited at intervals of one to two hours.

Because of the low flower availability, hummingbird species basically acted as low-reward trapliners in the studied grasslands (foraging strategies after Feinsinger & Colwell, 1978). Territorial foraging behavior was recorded only in the large clusters of

Sinningia allagophylla, *Clytolaema rubricauda* and *Stephanoxis lalandi* behaved territorially in these circumstances, and *Leucochloris albicollis* occasionally acted as a parasite in territories set by *Clytolaema rubricauda*. Thus, *Leucochloris albicollis* may alternate its foraging strategy from low-reward traplining to territory-parasitism in some cases.

G. MISCELLANEA

Many oil-collecting bees—mainly large bees belonging to *Centris*—were recorded pollinating *Byrsonima variabilis* (Fig. 2D–E). The mechanism for oil-collection in this species was similar to that recorded for other Malpighiaceae species (see Vogel, 1990). *Byrsonima variabilis* was also pollinated by small bees belonging to Apidae (Meliponinae) and Halictidae in search of pollen, but to a minor degree. Some oil-collecting bees also collected pollen on this *Byrsonima* Rich. ex Juss. species.

The nectar-flowers of *Tassadia subulata* were exclusively pollinated by syrphids, which carried the pollinia on their heads. The elaborate, small, ruby flowers of this species are typically myophilous (sensu Faegri & van der Pijl, 1979). Small bees were also associated with syrphids on the nectar-secreting flowers of *Senecio oleosus*, *Wahlenbergia brasiliensis*, and *Convolvulus crenatifolius* (Fig. 2F–G). The last two species bear bell-shaped, lilac/lavender flowers. Pollinators first fed on the nectar of these three species, although they also searched for pollen on them. Syrphids and small bees seemed to be co-pollinators of these species (syrphid/bee nectar-flower system).

H. SPECIES WHOSE POLLINATION SYSTEMS ARE DOUBTFUL

The flowers of 18 species were either not visited during the observation sessions or the role of their visitor in pollination was not clear. The results and brief discussions of these cases are presented herein.

Although many *Oncidium* Sw. species bear flowers that produce nonvolatile oils with a chemical composition suitable for larval nurturing by “Anthophoridae” bees (Reis et al., 2000; A. D. Faria, pers. comm.), only one single observation of a bee actively collecting oils on *Oncidium* flowers has been reported so far (Singer & Cocucci, 1999). We did not observe oil-collecting bees visiting flowers of *Oncidium* species (total 47 hr. of observation, Table 4). However, we collected an individual of *Monoeca* sp. indet. 1 (Tapinotaspidini) (Fig. 2J) and an individual of *Megachile aureiventris* Schrottky (Megachilidae) each carrying an *Oncidium* pollinarium attached to its head. During an observation session on *Lupinus*

relutinus flowers, a female individual of *Bombus*—after collecting the pollen of *Lupinus* L. flowers—quickly visited a flower of *Oncidium barbaceniae*. During this visit, the bee vibrated in a failed attempt to collect pollen. We did not collect this individual bumblebee but observed that the visited flower had no pollinia, indicating that this bee could have removed them. These observations indicate that bees in search of pollen could be acting as pollinators in these populations of *Oncidium*. Thus, in addition to the expected system involving oil-collecting bees, *Oncidium* flowers could be pollinated by deceit by pollen-collecting bees. The following aspects point to a pollination system by deceit in the studied populations: (1) bees in search of pollen visited their flowers; (2) bees of the “Anthophoridae” group intensively collected oil on *Byrsonima* flowers but were not recorded on flowers of the *Oncidium* species growing in the same patch; (3) visits by bees from any group were scarce on *Oncidium* flowers, and fruit production was very low in the three species. In short, pollination of the three species at Bocaina is unclear, and more comprehensive studies are required to understand the pollination biology of this genus.

The tubular flowers of *Calolisianthus pendulus* do not produce floral nectar, except for some rare flowers with minute nectarioles (sensu Vogel, 1998) located on petals. No visits to their flowers were recorded, and delayed self-pollination seems to ensure the reproduction of this species, as well as that of the other four studied gentians of Bocaina, which include the ornithophilous *Calolisianthus pedunculatus* with nectarless flowers (Fig. 4L) (see Freitas, 2004 for details).

Although the floral features of three species (*Mandevilla erecta*, *Habenaria parviflora*, and *Helia oblongifolia* [Fig. 2K]) point to phalaenophily and sphingophily (after Faegri & van der Pijl, 1979), no nocturnal moths were recorded visiting their flowers (Table 4). These species flower in the middle of the wet season (Table 1). The flowers have narrow greenish or yellowish tubes (spurs in *H. parviflora*), presenting both odor and nectar at night. The long-lived flowers of *H. oblongifolia* are spontaneously self-pollinated at the end of anthesis (Freitas, 2004). The other two species were rare in the studied areas. *Mandevilla erecta* bears large inflorescences with dozens of flowers, but we only recorded one fruit produced during three subsequent blooming seasons (from 1998 to 2000). Several *Habenaria parviflora* plants produced fruits in the study areas. Although this species is self-compatible, spontaneous self-pollination is improbable (Singer, 2001). It is pollinated by crepuscular crane-flies and nocturnal moths in an area at sea level by the São Paulo

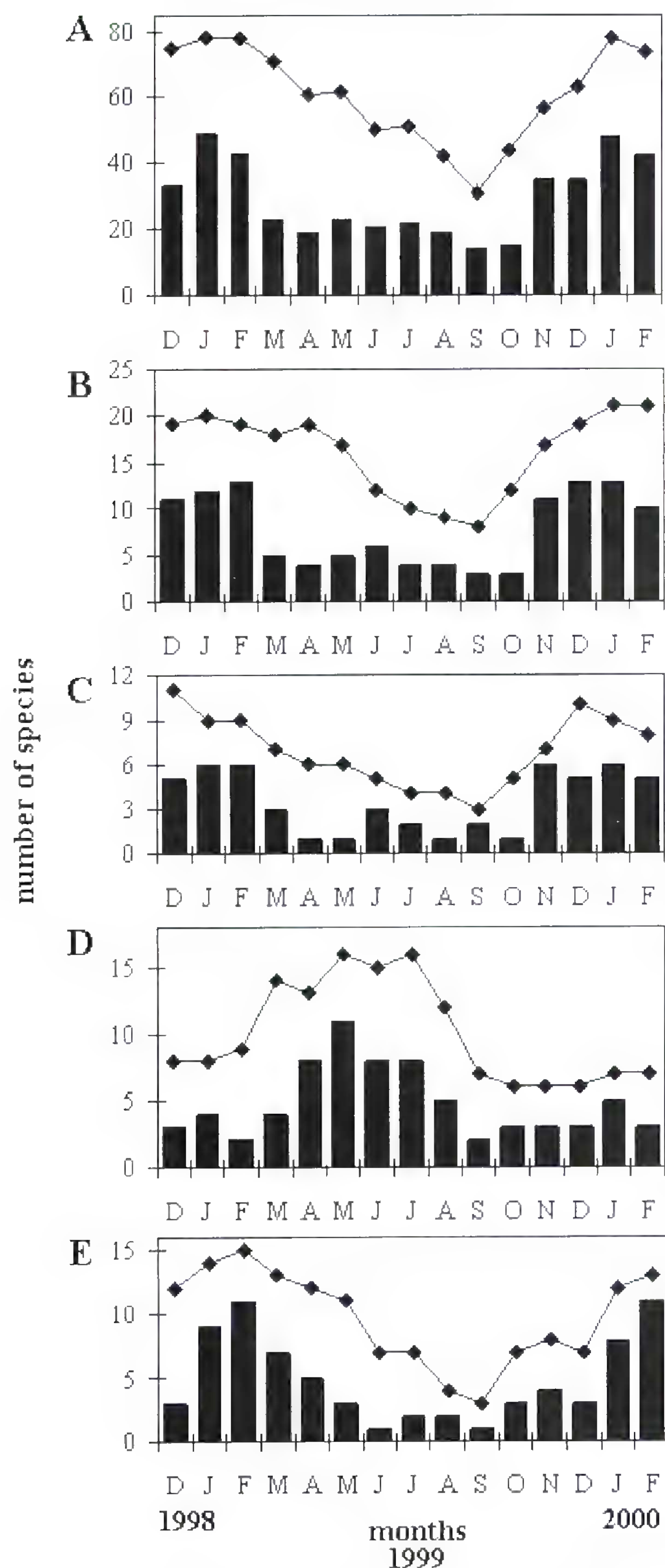


Figure 4. Number of species blooming (line) and in flowering peak (bars) from Dec. 1998 to Feb. 2000, in the Serra da Bocaina grasslands. —A. Distribution at the community level (n = 124). —B–E. Distribution of plant species of each pollination system. —B. Nectar-flowers pollinated mainly by small and large bees (n = 30). —C. Pollen-flowers pollinated by small and large bees (n = 15). —D. Nectar-flowers pollinated either by wasps or by wasps and dipterans (n = 22). —E. Nectar-flowers pollinated by several insect groups (SIG) (n = 20).

coastline (Singer, 2001). Results indicate that moths seldom use floral resources from grassland plants.

The two studied species of *Hypericum* L. have extended flowering times, with individual plants

flowering in different months year-round. The polyandrous flowers of both species are similar (Table 2). The flowers of the fourteen individuals of *Hypericum ternum* in the study area did not produce pollen, but all flowers developed fruits with well-developed seeds. Similar results were found for the ca. 40 individuals of *Hypericum brasiliense*. However, two individuals of the latter were found to produce flowers with pollen grains (ca. 95% viability) in December 1998. One of these plants had been followed since January 1998, and, curiously, it produced only flowers without pollen until December 1998. This capacity for sexual and apomictic reproduction within the same individual is named facultativism and may be environmentally influenced (Asker & Jerling, 1992). In the pollen-producing flowers of *Hypericum brasiliense*, self- and cross-pollen tubes grew down the style, but only crossed ones seemed to penetrate the ovule. We observed these pollen-producing individuals in December 1998 and January 1999 and found that insects, mainly syrphids and small bees, searched for pollen and pollinated their flowers (Table 4). Empty anthers were also observed in herbarium specimens of *Hypericum* species from lowland forest areas (V. Bittrich, pers. comm.). It is expected that *H. ternum* also occasionally produces pollen.

No floral visitors were registered during the 28 hr. of observation of the four *Leandra* Raddi species. There are records of apomixis and pollenless flowers in species of this genus (Goldenberg & Shepherd, 1998; R. Goldenberg, pers. comm.); thus the *Leandra* species at Bocaina may also be apomictic. Another Melastomataceae, *Microlicia isophylla*, was not visited either. This species is very common in grasslands and bears attractive flowers, with magenta petals and vivid yellow anthers. Their smooth pollen grains are highly viable and are produced in large quantity. Bees collecting pollen by vibration are the expected pollinators of this species, although it could also be apomictic.

The small, greenish flowers of *Eryngium canaliculatum* are very similar to those of *E. horridum*. Floral traits of *E. canaliculatum* point to a SIG pollination system, although only four visits by two species of beetles were recorded on these flowers. Further observations are necessary to ascertain their pollination system. We did not observe pollinators visiting the showy flowers of *Chromolaena xylorrhiza* and *Epidendrum secundum* that fit in the melittophilous syndrome.

DEGREE OF SPECIALIZATION OF POLLINATION SYSTEMS

Around one third of the plant species were pollinated by only one pollinator group (monophilous, Table 6). For 50 out the 70 species pollinated by two

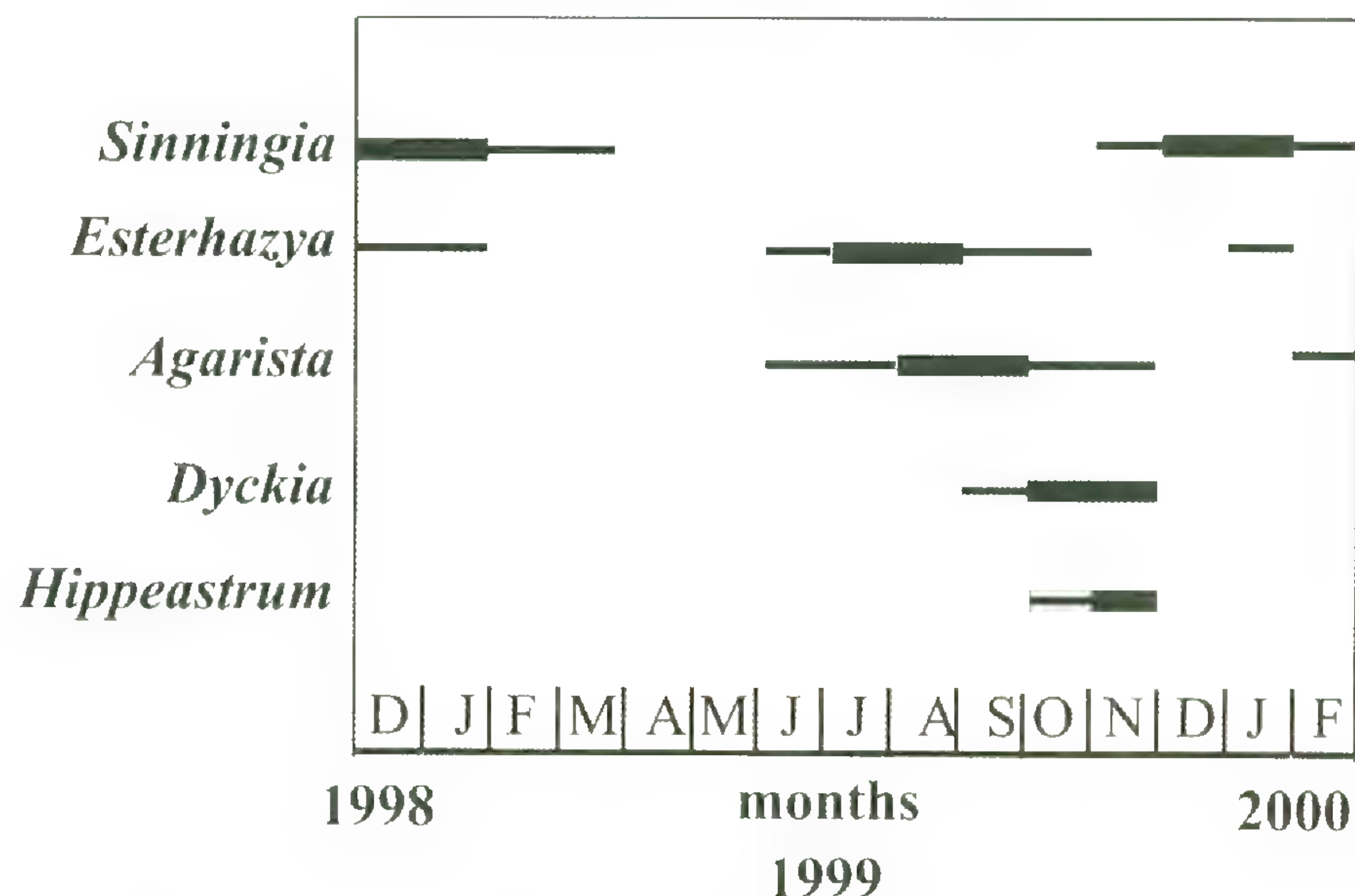


Figure 5. Flowering patterns of the five hummingbird-pollinated species from the Serra da Bocaina grasslands from December 1998 to February 2000. Thin and thick lines indicate, respectively, flowering time and flowering peak. Plant species are abbreviated according to their genus (see Table 1 for species epithet).

to six pollinator groups, we were able to determine one or two insect groups acting as main pollen vectors (oligophilous and polyphilous). The remaining 20 species were holophilous, since they presented no dominant pollinator group. Monophily dominates among pollen-bee flowers, and oligophily among syrphid and bee pollen-flowers. Species belonging to the bee nectar-flowers and wasp/fly flowers systems are more equitably distributed among monophily, oligophily, and polyphily (Table 6).

More than half of the species pollinated by small and large bees are monophilous or oligophilous (Table 6). In contrast, most species pollinated by flies, butterflies, and beetles are holophilous. The species pollinated by wasps and syrphids are better distributed among oligophily, polyphily, and holophily.

FLOWERING PHENOLOGY

Flowering duration in grasslands was long (mean 5.5 ± 2.92 months, $n = 124$), and the mean flowering peak duration was 2.6 ± 1.56 months ($n = 124$) (Table 1). Flowering pattern in this community was seasonal, with a peak during the middle of the wet season (Fig. 4A). Over 60% of the species flowered in January and February, and ca. one-third of the species were at their flowering peak during these two months. There was a drastic reduction in flowering during the end of the dry season/beginning of the wet season (Aug.–Oct.). The fire that occurred in one area in September 1999 may have only slightly affected these general patterns, because only eight species from this area did not occur in at least one of the other two studied areas (see Table 1).

Blooming patterns of the species with nectar- or pollen-flowers pollinated by bees followed the pattern

observed in the community (Fig. 4A–C). However, there was a slight increase of species at peak flowering in June (Fig. 4B–C). In contrast, most species with nectar-flowers pollinated either by wasps or by wasps and dipterans reached their flowering peak during the dry season (Fig. 4D). Wasps are very important pollinators during that season. For example, 11 out of 23 species at their flowering peak in May, 1999 were exclusively or mainly pollinated by wasps (Fig. 4A, D). The flowering pattern of SIG species resembles the general pattern of the community, but a few plants at their flowering peak were recorded throughout the year (Fig. 4A, E). The flowering of the five hummingbird-pollinated species concentrated at the beginning of the wet season (Fig. 5). No plants flowered in April and May, and no plants were at their flowering peaks during five months of the year.

DISCUSSION

Although Martinelli (1989) reported a total of 215 flowering species in the Bocaina grasslands, we collected ca. 260 species. About 20% of these 260 species belong to the families Poaceae, Cyperaceae, and Juncaceae and are anemophilous. This study thus included around 60% (124 species) of the ca. 210 animal-pollinated species from the Bocaina grasslands, and pollinators were determined for about half of these zoophilous species (106 species). In addition, ca. 80% of the 47 plant families found in the Bocaina grasslands were represented in this study, so that our sample was fairly representative of these high-altitude grasslands.

We carried out intensive pollinator observations for some plant species and brief ones for many others, as expected in studies on plant-pollinator interactions at

the community level which encompass many species with low population density (see Momose et al., 1998). Both the short observation times and the generally low flower visitation rates explain why we may have failed to ascertain the typical pollination system of some species in the Bocaina grasslands. However, since we used broad categories to describe the pollination systems, we may outline general interaction trends in this community and establish general comparisons.

There are no comparative data on the floral and pollination biology of any other high-altitude grassland areas in southeastern Brazil. However, community level pollination data from vegetational types with both abiotic similarities and strong biogeographic connections are available. These include the high temperate Chilean Andes, especially in the sub-Andean scrub zone (Arroyo et al., 1982), the Venezuelan Guiana high-altitude shrubland or *arbustal* (Ramírez, 1989), the Brazilian open savannas or *cerrado* (Barbosa, 1997; see also Silberbauer-Gottsberger & Gottsberger, 1988 and Oliveira & Gibbs, 2000 for other *cerrado* physiognomies), and, to some extent, data from the Brazilian *campo rupestre* (Faria, 1994). We focus our discussion on comparisons between these formations and the Bocaina grasslands.

FLORAL TRAITS

Flowers with light colors—including greenish, pink, and white color groups—are well represented in the grasslands, resembling the *arbustal* and *cerrado* communities, in which light-colored flowers predominate (Silberbauer-Gottsberger & Gottsberger, 1988; Ramírez, 1989; Barbosa, 1997). However, more than half of the species at Bocaina have showy flowers (violet, yellow, and red color groups). This dominance is due to the presence of Asteraceae and Melastomataceae, with their showy violet-colored flowers, in these grasslands. Furthermore, greenish flowers were more continuously distributed throughout the year, in contrast to violet flowers that are concentrated during the wet months. Using canonical discriminant analysis (L. Freitas, unpubl. res.), we only detected a weak relationship between floral color and the frequency of visits for each pollinator group in the community. Red flowers were strongly associated with hummingbird visitation and greenish flowers weakly associated with visitations primarily by beetles and wasps. Although we used the human color spectrum, such results for insect responses to flower color resemble the general trends detected by Chittka et al. (1994) and Waser et al. (1996), who found no statistical differences among insect pollinator groups, at the order level, in terms of the colors of the visited flowers.

The prevalence of nectar as the main floral resource at Bocaina was recorded in other grassy communities (Arroyo et al., 1982; Ramírez, 1989; Faria, 1994; Barbosa, 1997). In fact, nectar-flowers are the most important flower class among angiosperms in general, because most pollinator groups are nectar consumers (Endress, 1994). The percentage of pollen-flowers at Bocaina was similar to that registered in the *campo rupestre* (Faria, 1994) and the *cerrado* (Barbosa, 1997). Melastomataceae species are the most important pollen-flowers at Bocaina, as well as in the *campo rupestre* (Faria, 1994). Species of this family are also important pollen sources in the *arbustal* (Ramírez, 1989). However, species of other families, such as Leguminosae and Myrtaceae, constitute the chief sources of pollen in the *cerrado* (Barbosa, 1997). Malpighiaceae are represented by several species in the *campo rupestre* and the *cerrado* (Faria, 1994; Barbosa, 1997), which explains why oil-flowers are more frequent in those communities than in the Bocaina grasslands.

Although small flowers predominate in the *arbustal* and the *cerrado* (Ramírez, 1989; Barbosa, 1997), the flowers of these two communities are larger than those at Bocaina. As for the floral color patterns, the relative predominance of Asteraceae in the community strongly influences the floral size patterns. The prevalence of small tubular flowers secreting nectar at Bocaina is a direct reflection of the number of Asteraceae presenting these floral traits and apparently not the result of selection by the local pollinator agents.

The prevalence of hermaphroditic flowers is typical of angiosperms, and, consequently, characteristic of most communities (Ramírez, 1993), including the grassland flora at Bocaina. However, many of the hermaphroditic flowers exhibited spatial or temporal separation of the male and female functions, through dichogamy, herkogamy, or heterostyly. In fact, a high frequency of dichogamy (protandry) is expected in a flora dominated by Asteraceae, owing to the frequent presence of secondary pollen presentation on the style among the Asterales (see Yeo, 1993). In addition, the female ray-florets of many Asteraceae species impart a state of protogyny to the head as a whole.

All the dioecious species of the studied community belong to the genus *Baccharis*, which was primarily associated with wasp pollination. Dioecy has often been associated with a generalist mode of pollination by small opportunistic insects (Bawa, 1994; but see Renner & Feil, 1993) or with wind pollination (Culley et al., 2002). Although this study did not focus on abiotic pollination, some evidence suggests the existence of ambophily among the studied taxa, in

which wind could be a pollen vector in addition to insects (e.g., *Croton dichrous*). The species of *Baccharis* may also fit in this category, as female heads have well-exposed stigmata and male flowers produce small pollen grains. Furthermore, we found pollen grains of *Baccharis* species adhered to microscope slides covered by glycerol, during exploratory experiments at the study sites, and most species of this genus flower during the winter, when insect activity is reduced. Pollinator limitation, dry weather, and the presence of recurrent wind in the winter could favor the evolution of anemophily and ambophily in the high-altitude grasslands (see Culley et al., 2002).

POLLINATION AGENTS

Hymenopterans, markedly small bees, are the predominant pollinators in the Bocaina grasslands, as well as in the *cerrado*, *arbustal*, and Subandean zone (Arroyo et al., 1982; Ramírez, 1989; Barbosa, 1997). Bees have been reported as the main pollinators for most communities (e.g., Moldenke, 1976; Kevan & Baker, 1983; Roubik, 1989; Bawa, 1990; Momose et al., 1998; Nakano & Washitani, 2003; Ramírez, 2004), and different patterns—for example the dominance of dipterans—seem to be restricted to very singular habitats, such as Arctic and alpine areas or oceanic islands (e.g., Kevan & Baker, 1983; Primack & Inouye, 1993; Anderson et al., 2001). However, certain communities with similar percentages of bee pollination may exhibit marked differences among their general patterns of pollination. Bees belonging to different groups show great variation in, for instance, their preferences, abilities, and behavior on flowers (see Roubik, 1989), and such variation is expected to lead to different pollination patterns among communities with distinct bee faunas.

The two main functional groups of bees in the Bocaina grasslands are the large bumblebees and small halictid bees. Agents of one or both of these groups were among the pollinators of 67 out of the 106 species (63%). *Bombus* and Halictidae species pollinated, respectively, 78% of the large bee-pollinated species (28 out of 36), and 76% of the small bee-pollinated species (54 out of 71). Both bee groups exhibited a generalist foraging behavior, visiting flowers of different shapes, sizes, and colors, which, in many cases, were also pollinated by other groups. An illustrative example is that of an individual of *Bombus atratus* observed visiting the violaceous flowers of seven species, belonging to Asteraceae, Lamiaceae, and Rubiaceae, in a single foraging trip (for ca. three min). Such generalist behavior is typical

of the Brazilian species of *Bombus* (Alves-dos-Santos, 1999; Barbola et al., 2000). Bumblebees pollinated most of the large bee-pollinated species at Bocaina and predominated in almost half of them, including the richest ones in terms of nectar, such as *Oxypetalum sublanatum*, *Lobelia camporum*, *Cuphea glutinosa*, and *Verbena hirta*. Moreover, these bees showed a trapline behavior, favoring pollen dispersal at great distances. Considered together, the variety of visited flowers (including nectar- and pollen-flowers), foraging behavior, dominance of the richest resources, and year-round activity make bumblebees the main pollinators of the plant group related to large bee pollination. Bumblebees are known to be one of the most important pollinators in cool temperate climates (Kevan et al., 1993; Nakano & Washitani, 2003), and the harsh climatic conditions, for a tropical place, that characterize the Brazilian high-altitude grasslands may be related to the high importance of bumblebee pollination at Bocaina.

Pseudagapostemon cyaneus (Halictidae) visited only flowers of *Mikania lundiana* and *Senecio oleosus* (Asteraceae) at Bocaina (Fig. 2G). Similarly, this bee species was a narrow oligolectic associated to *S. oleosus* flowers, in a grassland area at Lapa, State of Paraná, southern Brazil (Barbola et al., 2000). *Pseudagapostemon cyaneus* occurs from southernmost Brazil to the State of São Paulo. In this last region, it is only reported above 1000 m (Cure, 1989). The particular interaction between *Senecio oleosus* and *Pseudagapostemon cyaneus* at both Bocaina and Lapa is one of the most illustrative examples of biogeographic connections between the mountain ranges of southeastern Brazil and the cool lowland areas in southernmost regions (see Behling, 1997).

Pollination by wasps has been observed in some highly specialized and infrequent cases (e.g., *Ophrys* L., *Ficus* L.), as well as among generalist plants pollinated by several insects (Faegri & van der Pijl, 1979). In most communities, wasps have been reported as minor agents (e.g., Arroyo et al., 1982; Bawa et al., 1985; Silberbauer-Gottsberger & Gottsberger, 1988; Momose et al., 1998; Oliveira & Gibbs, 2000). In contrast, wasps pollinated 45% of the species in the Bocaina grasslands and acted as the exclusive or main pollinators of more than 20% of the animal-pollinated species in this community (Table 5). Although wasps have their importance in the pollination of *cerrado* and *arbustal*, they are the exclusive pollinators of only a few species in these communities (Ramírez, 1989; Barbosa, 1997). In fact, as far as we know, such importance of wasp pollination as observed in the Bocaina grasslands has never been reported for any other ecosystem. Whether the wasps are minor pollinators or their role

in pollination has been neglected in Neotropical communities is still an inadequately explored issue that deserves further study. However, at least in some subtropical habitats, the rates of floral visitation by wasps, as well as their probable importance as pollinators at the community level, seem to have been underestimated (P. Feinsinger, pers. comm.).

At Bocaina, lepidopterans were generally copollinators of species with a generalist pollination system or secondary pollinators of species pollinated mainly by bees. Similar results were found in *cerrado* and *arbustal* areas (Ramírez, 1989; Barbosa, 1997; Oliveira & Gibbs, 2000). However, butterflies are very important pollinators in the open vegetation of the Chilean Andes, especially in the subnival zone (Arroyo et al., 1982). In spite of the scarcity of their visits to flowers, butterflies (mainly HesperIIDae) may have an important role in the gene flow of many species at Bocaina, transferring pollen at long distances due to their traplining behavior. Despite some highly specialized cases, such as those related to long-tongued flies in South Africa (e.g., Goldblatt et al., 1995), fly pollination has been considered mostly unspecialized, since flies do not feed their young and may have other food sources than flowers (Kearns, 1992; Proctor et al., 1996). Most species pollinated by the three most important fly groups at Bocaina—Syrphidae, Tachinidae, and Bombyliidae—have small nectar-flowers that were pollinated by several agents. However, syrphids, associated with small bees, were the pollinators of many species, particularly those with pollen-flowers. These last species present monophilous or oligophilous pollination systems. This result shows that pollination by flies can be specialized even in the absence of extreme proboscis elongation. If we consider the species for which syrphids and other dipterans are either the main or the exclusive pollinator, the percentage of species pollinated by flies at Bocaina is similar to that found in *cerrado* and *arbustal* areas (Ramírez, 1989; Barbosa, 1997). Nevertheless, in the Chilean Andes, myophily is more common (Arroyo et al., 1982). The great importance of flies and butterflies in the Chilean Andes, as compared to the other communities considered here, probably reflects the unfavorable climatic conditions for bee activity in the Andes (Arroyo et al., 1982; see also Kevan, 1975 and Kearns, 1992). In the Bocaina grasslands, climatic conditions are not harsh enough to limit the development of bees, which dominate the pollination in this community.

At Bocaina, the percentage of hummingbird-pollinated species is similar to that observed in *cerrado* areas (Barbosa, 1997), but it is lower than that of other high-altitude communities, such as *arbustal*

(12%) (Ramírez, 1989) and *campo rupestre* areas (10%) (Faria, 1994). In the Bocaina grasslands, ornithophilous species constitute secondary nectar sources for hummingbirds that find their main nectar sources in the surrounding high-altitude forest (Sazima et al., 1996; Freitas & Sazima, 2001). Two factors, at least, support this idea. First, in these grasslands, no ornithophilous species were flowering in April or May or were in their blooming peak during February to June. Therefore, this community would be unable to sustain hummingbirds throughout the year. Secondly, the five ornithophilous species were seldom visited by hummingbirds, while hummingbirds intensively fed on ca. 30 species of the surrounding forest areas (Sazima et al., 1996; Buzato et al., 2000; L. Freitas, pers. obs.). Hence, at Bocaina, the continued replacement of forest areas by grasslands—mainly because of fires—is a risk factor for populations of the five hummingbird species observed in the grasslands, in particular for *Stephanoxis l. lalandi*, which lives exclusively in some high-altitude areas of southeastern Brazil (Grantsau, 1989; Sazima et al., 1996).

We did not observe any pollination by either bats or other mammals in the Bocaina grasslands. Moreover, no species were collected with floral features in accordance with the mammal pollination syndromes, suggesting the absence of such pollination systems in these grasslands. Reports of bat-pollinated species from mesic habitats in high-altitude grasslands are restricted to three Bromeliaceae species (Martinelli, 1994, 1997). In contrast, bat pollination is well represented in the high-altitude forest areas that surround the grasslands (Sazima et al., 1999).

The Bocaina grasslands also lack perfume flowers, another highly specialized pollination system related to male euglossine bees (e.g., Sazima et al., 1993). Euglossine bees have restricted altitudinal limits of distribution (Roubik, 1989), and aromatic compounds traps did not detect any such bee in the Bocaina high-altitude grasslands.

In contrast to bats, nocturnal pollination by moths is expected since the Bocaina grasslands present at least three species adapted to it. However, we did not observe these pollinator agents, and the low fruit set in *Mandevilla erecta* indicate low—perhaps unpredictable—rates of flower visits by nocturnal moths in these habitats. As suggested for the *cerrado* area (Oliveira & Gibbs, 2000), strong winds at the study areas may be harmful to the moth pollinating species. In addition, the restricted flowering time of the species that might be moth-pollinated in the Bocaina grasslands may be linked to migrating pollinator agents, which would increase the difficulty of observing pollinators.

FLOWERING IN RELATION TO POLLINATORS

At Bocaina, the bees of all families reduced their activity during the dry season. Such reduction in the number of bee species and individuals in activity during the winter was observed in connected ecosystems in southern Brazil (Alves-dos-Santos, 1999; Barbola et al., 2000) and is related to several factors, such as the reproductive phenology of bee species, climatic restriction for flying, and flower availability. The flowering patterns of species pollinated mainly by bees followed the pattern of the community as a whole. Thus, flower resources for bees, especially large bees, decrease during the dry season. In addition, such climatic conditions as low temperatures, low precipitation, and occasional frosts are apparently unfavorable for flowering during the winter months. Moreover, the flowering pattern of species with either nectar- or pollen-flowers overlapped, and this result indicates reciprocity between the availability of resources for adults (i.e., nectar) and larvae (i.e., pollen) of bees at the community level, although it is difficult to ascertain if these patterns are not casual.

In contrast to bees, social wasps showed a more constant activity pattern throughout the year, and pollination by this group was prominent during the dry season at Bocaina. Because, in this area, several species that are pollinated mainly by wasps are apparently also pollinated by wind, anemophily, rather than pollination by wasps, may be an ultimate factor driving flowering concentration during the dry season in this group of species. If we consider the flowering phenology of species belonging to the most representative pollination systems at Bocaina, only the few species that flower during the dry season (wet season for wasp-pollinated species) seem to be fundamental to support populations of insects. For example, the floral nectar of the nearly year-long-flowering species *Cuphea glutinosa*, *Galianthe brasiliensis*, and *Verbena hirta*, and the winter-flowering *Eremanthus erythropappus* constitutes a keystone plant resource (sensu van Schaik et al., 1993) for bee pollinators during the winter. These four species are large shrubs or treelets (*E. erythropappus*) with many flowers and are particularly important for bumblebees during this period of low flower availability.

Anthropogenic fires are common during the dry season in the Bocaina grasslands. A few months after fires, we observed mass-flowering of several species such as *Sinningia allagophylla*, *Microlicia isophylla*, *Tibouchina frigidula*, *T. minor*, *Galianthe angustifolia*, and *Xyris asperulla*. Flowering controlled by fires is a well-known and widespread phenomenon among

cerrado species (Coutinho, 1990), but, according to Safford (2001), based on his observation in the Serra do Caparaó, it is not characteristic of the Brazilian high-altitude grasslands. A possible reason for the difference between Safford's observation and ours is that the ecological similarities between *cerrado* and high-altitude grasslands may be more pronounced at Bocaina, due to intense fire regimes, than at other high-altitude grasslands of southeastern Brazil (see Safford, 1999a, 2001 and also Martinelli, 1989 for floristic comparison). In this sense, Bocaina grasslands may be more pyrogenic than other grassland areas, such as those from Pico do Itatiaia, Serra dos Órgãos, and Serra do Caparaó.

SPECIALIST VERSUS GENERALIST POLLINATION SYSTEMS

The traditional view in studies based on the syndrome concept (see Faegri & van der Pijl, 1979) supports the idea that pollination systems mostly tend toward increased specialization. Such a view has been questioned in more recent times due to evidence of more widespread generalization in pollination systems (e.g., McDade, 1992; Waser et al., 1996; Herrera, 1996; Ollerton, 1996; Olesen & Jordano, 2002). These field observations of regional or local flora contexts show that many plant species are visited by many animal species, and, as a result, the mean number of species of animal visitors per plant species is high. Alternatively, we used the number of functional groups of pollinators per plant species as a parameter of the degree of specialization of the pollination systems at Bocaina. Functional groups are more suited to this purpose than pollinator species for several reasons (see Fenster et al., 2004). Different species of the same functional group, for instance, are expected to exert similar selection pressures on the floral traits related to pollination mechanisms. Thus, considering such species as distinct entities generates some artificiality. Another factor is that the number of pollinator species belonging to each functional group varies drastically within a local community, as does the species richness of a given functional group among distinct communities or regions. Thus, plant species pollinated by more diverse functional groups would simply appear more generalized, despite the biological proprieties of their pollination system.

Ramírez (2002) used the functional group approach to compare the degree of specialization of nine tropical and temperate communities. The mean number of pollinator groups per plant species ranged from 1.0, in a beach dune vegetation of northern Brazil, to 1.85, in the forest of the Venezuelan Central Plain. Using the same functional groups as Ramírez (2002), the Bocaina grasslands has a mean of 2.09

pollinator types per plant, probably one of the highest values for worldwide floras. The higher degree of generalization at Bocaina is also evident if we consider the distribution of species along the four specificity categories (i.e., monophily to holophily). Monophily, as used here, encompasses both the monophily and oligophily categories of Ramírez (2002). More than half of the species, at least, belonged to these two categories in six tropical communities (between 54% and 100%; Ramírez, 2002), in contrast to the Bocaina grasslands where one third of the species are monophilous.

However, the functional group approach to determine the specialization degree of pollination systems may also induce some artificiality. One well-demonstrated theory is that different pollinators of a given plant species may vary in their pollinating abilities in such a way that this plant species may effectively specialize on its most efficient visitor (Stebbins, 1970; Schemske & Horvitz, 1984; Ollerton, 1996; Fenster et al., 2004). Another point is that the definition of functional groups of pollinators (e.g., small bees, moths, bats) is typically based on systematic boundaries. Thus, two pollinators in distinct orders are in general placed in different functional groups, even if they probably exert similar selection pressures on floral traits. For example, at Bocaina, some of the pollen-flowers are pollinated by syrphids and small bees and some of the nectar-flowers are pollinated by small bees and wasps; we named this situation oligophily. If we combine monophily and oligophily, we conclude that almost two thirds of the zoophilous species in this community present a specialization onto functional groups. Likewise, a reanalysis of the dataset from the flora of Carlinville, Illinois, indicated that about 75% of the species showed specialized pollination systems (Fenster et al., 2004), contrasting with a previous conclusion of generalization predominance in this community (Waser et al., 1996), which was based on the number of pollinator species per plant species.

Even using the above perspective of “wide functional groups” (i.e., oligophily considered as a specialized system), a considerable degree of generalization (more than one-third of species) is found in the Bocaina grasslands. Broadly, generalization is predicted as long as temporal and spatial variance in pollinator quality is appreciable; different pollinator agents do not fluctuate in unison and are similar in their pollination effectiveness (Waser et al., 1996). Thus, the climatic conditions of the high-altitude grasslands may favor the occurrence of generalists at Bocaina. Generalization in pollination systems seems to be more frequent in naturally inclement or unstable areas, in the modern agricul-

tural-urban mosaics or human surroundings, and among short-lived plants (Vogel & Westerkamp, 1991; Johnson & Steiner, 2000, 2003). In this sense, frequent fires may be an additional factor that makes the environment harsher for specialists (both plants and animals) in the Bocaina grasslands.

Generalist pollination systems have often been characterized by small and white or greenish-colored flowers pollinated by small insects, the diverse small insect (d.s.i) syndrome of Bawa et al. (1985). However, some of the small greenish flowers at Bocaina present highly specialized pollination systems (e.g., *Gonioanthela hilariana*), and the pollination of some holophilous species involves such large insects as large bees, wasps, and butterflies. Therefore, the degree of generalization should not be inferred from the sizes of flowers and pollinators, as previously postulated by Ramírez (1989). Although represented mainly by the families Asteraceae and Rubiaceae, the holophilous species at Bocaina vary in both their floral traits and their flowering phenology. In addition, some genera with holophilous species also have monophilous or oligophilous species: for example, wasp pollination in *Baccharis* and *Borreria* G. Mey. and bee and butterfly pollination in *Vernonia* Schreb. and in the *Eupatorium* L. alliance. For such genera, the floral features that determine whether a few or several pollinator groups are attracted to the flowers of specialists or generalists, respectively, remain unclear. Moreover, since the degree of specialization/generalization of pollination systems may be influenced by factors such as plant life history, phylogenetic constraints, vegetation strata, successional status, plant abundance, breeding system, and local fauna (Stebbins, 1970; Vogel & Westerkamp, 1991; Waser et al., 1996; Ollerton, 1996; Johnson & Steiner, 2000, 2003; Ramírez, 2002, 2004; Nakano & Washitani, 2003; Fenster et al., 2004), floral traits alone may be inadequate to address this issue properly.

CONCLUDING REMARKS

The correlation between certain taxa and particular ecological conditions may enhance the abundance of given plant groups. Thus, ecological attributes, unrelated to sexual reproduction, may promote certain taxonomic groups with particular reproductive traits, and hence, may bias the frequency distribution of these traits in the community (Vogel & Westerkamp, 1991; Ramírez, 1993). Apart from the wind-pollinated species of Poaceae and Cyperaceae, the Bocaina grasslands are dominated by species of Asteraceae, which strongly influence the floral features (i.e., short tubular flowers that offer nectar and have exposed reproductive parts) at the community level. In these grasslands, general trends related to the types of

pollination systems and degree of generalization may be connected to the phylogenetic floral trends of species with certain abilities—not necessarily related to pollination—to occupy these habitats, such as short living-cycles and adaptations to frost, low mean temperature, high daily temperature variation, acidic soils, and, more recently, some kind of adaptation to fire (see Safford, 1999a).

Biogeographic and palynologic studies indicate that high-altitude grasslands in southern and southeastern Brazil have to be understood as relicts of the Pleistocene cold and dry climates and of the early- and mid-Holocene warm and dry climates (Behling, 1997). Because of their relatively recent origin, these grasslands are unlikely to have produced highly coevolved plant communities, although some relictual plant-pollinator interactions could have been retained in cases where both the plant and its pollinator colonized the mountain tops. These grasslands are linked to episodes of expansion and retraction due to glacial events during the Quaternary (Behling, 1997; Safford, 1999a). Such a situation may have favored species with the ability to occupy new habitats quickly. Dependence on a few specialized pollinators may be less suitable than more generalist pollination systems in the occupation of a new habitat, because previous pollinator agents may be left behind. In fact, generalized pollination systems may have been an ecological advantage for plants colonizing post-glacial landscapes (Johnson & Steiner, 2000, 2003). Alternatively, for those species with more specialized pollination systems, some floral traits that are frequent at Bocaina, such as spontaneous self-pollination mechanisms and long-lived flowers, may be advantageous to both plant establishment and maintenance in these grasslands characterized by unpredictable and scarce pollinators.

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